AGONISTIC AND SEXUAL COMMUNICATION
IN THE
LITTLE BLUE PENGUINS, Eudyptula minor

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Joseph Rupert Waas

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Dedicated to my parents, Anne and Rupert Waas, for their love and encouragement
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The little blue penguin, *Eudyptula minor*, was used to examine three specific issues in animal communication.

(1) Ethologists have traditionally viewed social repertoires as being fixed and invariable. In contrast, my analysis of agonistic behaviour of little blue penguins occupying two different habitats revealed significant variation in repertoire size and form. Cave-dwellers, which had large and complex repertoires, occupied open colonies characterized by high interaction rates. Burrow-dwellers, which had small repertoires, occupied colonies in which conspecifics were isolated from one another and rarely interacted. Despite higher interaction rates, cave-dwellers attacked one another less often and used overtly aggressive behaviours with shorter durations than did burrow-dwellers. The results suggest that the size and form of repertoires may be mediated by the social and physical properties of occupied habitats. Large repertoires may reduce the proportion of encounters leading to overt aggression where interaction rates are high.

(2) Theoretical models of aggressive communication suggest that animals are unlikely to use aggressive displays to signal motivation. Using lag sequential analysis, I examined over 2000 agonistic interactions between cave-dwelling penguins. The results suggested that aggressive displays differ in how costly they are to perform (i.e. as measured by the risk of escalation) and that high cost displays were more effective in deterring opponents than low cost displays. I argue that animals can signal motivation by taking risks during interactions, as demonstrated by their choice of display.

(3) The social facilitation of courtship behaviour is a widely assumed but rarely demonstrated process thought to be related to breeding synchrony. Using a playback experiment, I demonstrated that the acoustic components of penguin displays facilitated courtship behaviour from perceiving conspecifics. I argue that social facilitation may alter the availability of social stimuli and cluster acts of copulation, both of which may influence the timing and synchrony of breeding.
INTRODUCTION

Current research on social behaviour is progressing along two separate, but interrelated, pathways (Emlen 1980). The first and most neglected area of research is concerned with identifying and understanding variation in the form and organization of social behaviour associated with environmental heterogeneity (i.e. socio-ecology). The second branch of research is primarily concerned with identifying and understanding the types of behavioural interactions that occur between animals living under a common set of circumstances (i.e. mainstream ethology and behavioural ecology).

In the present study, I examined the communicatory behaviour of little blue penguins, *Eudyptula minor*, and considered issues pertaining to both branches of research identified above. The research addressed several key issues in animal communication for which little blue penguins were opportune subjects. The ultimate goal of this study was to advance our knowledge of factors (be they functional, causal, developmental or historical; Tinbergen 1963) contributing to the form and operation of communication systems found in the wild.

The main body of the thesis is composed of three chapters. Each chapter was written up as a separate and independent research paper in a format used by the journal *Animal Behaviour*. This approach has led to some overlap in information, particularly in the Methods and Introduction sections of each chapter, but I attempted to restrict overlap as far as possible. I will briefly outline the topics covered in each chapter below. A more detailed description of specific questions and hypotheses for each paper are provided in the Introductions to each chapter.

In the first paper (Chapter I), I report on the findings of a study designed to investigate relationships between intraspecific variation in social behaviour and environmental heterogeneity. The study identified dramatic differences in the agonistic repertoires used by little blue penguins inhabiting two contrasting breeding habitats. I discuss social and physical factors that might contribute to intraspecific variation in the social repertoires, and consider the possible significance of flexible social systems for little blue penguins.

In the second paper (Chapter II), I continue the theme of agonistic behaviour, but shift to the study of communication during the interactions of penguins living within a single social system. This paper examines the
controversial issue of information content in agonistic displays. Using lag sequential analysis (Sackett 1979), I examined the aggressive interactions of little blue penguins to determine whether aggressive displays differed in effectiveness and whether displays predict the signalling animal's next behaviour. The physical properties of displays were examined to determine why certain behaviours were more effective in deterring opponents than others.

In the third paper (Chapter III), I continue the study of communicatory processes during social interaction, but shift from agonistic to sexual behaviour. The paper examines the social facilitation of courtship displays used by little blue penguins. Social facilitation is a widely assumed but rarely demonstrated process, thought to be related to breeding synchrony. I used playback experiments to determine whether the acoustic components of displays used by little blue penguins facilitated courtship behaviour from perceiving conspecifics. I suggest that social facilitation may alter the availability of social stimuli and cluster acts of copulation, both of which may influence the timing and synchrony of breeding.

**Background: Ecology and Social Organization**

Little blue penguins are the smallest of all living penguin species and are the sole members of the genus *Eudyptula*. The species breeds in a wide variety of habitats on the mainland and offshore islands of southern Australia and New Zealand, including the Chatham Islands. Most of my research was conducted on penguins breeding on Banks Peninsula (central east coast of New Zealand's South Island) and Motunau Island (80 km north of Banks Peninsula and 1.5 km off the east coast of the South Island). The little blue penguins breeding there have been designated sub-specific status (i.e. the 'white-flippered penguin', *E. m. albosignata*; Kinsky & Falla 1976), but this classification is controversial (e.g. Merridith & Sin 1988).

There are several published (e.g. Kinsky 1960; Reilly & Balmford 1975; Gales 1985) and unpublished (e.g. Hodgson 1975; Jones 1978; Gales 1984) accounts of the breeding ecology of little blue penguins. A comparison of these studies indicates that the breeding biology of little blue penguins is highly variable over their breeding range. For this reason, I shall limit my discussion of breeding ecology to birds inhabiting Banks Peninsula and Motunau Island. Unfortunately, there are no detailed published accounts of the penguins breeding in these areas (but see O'Brien 1940) so
I have had to base the present overview on unpublished data collected during an 18 year study by Dr. C.N. Challies.

Little blue penguins are monogamous and long-lived (i.e. c. 15-20 years). Individuals usually start breeding by the time they reach three to four years of age, but some bred as two-year olds. Breeders commonly remained with the same partner for several years or, in some cases, for life. However, 'divorce' did occur, and it usually took the form of mate swaps between adjacent nest sites. Established breeding pairs tended to return to the same nest site for several consecutive years. There is little sexual dimorphism, although males are larger on average (Kinsky & Falla 1976).

Little blue penguins always bred under cover, for example, in caves, burrows, or under dense vegetation. The penguins tended to restrict movement and most social interactions on land to night time, often arriving on shore just after dusk. Breeding formations were highly variable, and they appeared to be partially dependent on habitat type. I studied little blue penguins in two distinct habitat types: caves and burrows (Chapter I). In caves, breeding pairs nested in tight aggregations (i.e. nests c. 1-2 m apart) with little or no physical barriers between nesting sites. In burrow habitats, breeding pairs nested solitarily or in semi-colonial formations (nests c. 2-5 m or more apart).

The breeding season on Banks Peninsula typically began in late April or early May in both cave and burrow habitats. In the early part of the season, unmated males attracted females using a sexual display that I refer to as the Solo Call (see Chapter III). In burrow habitats, males called solitarily from between rocks along the shore line just below breeding areas and rarely interacted with one another. In cave habitats, unmated males moved directly into central non-breeding areas of the cave, and they either called solitarily or formed small calling clubs (3-6 males). Aggressive interactions between club males in caves were common. It should be noted, however, that the mate attraction behaviour of males appears to be variable among populations. For example, on Phillip Island (Victoria, Australia) unmated males established themselves at territories before attracting partners (J.M. Cullen & P. Dann, personal communication).

Once a female was attracted, the new pair 'kept company' and performed sexual displays before moving away from non-breeding areas to search for a nest site. Aggressive interactions between searching pairs and birds with established nest sites were particularly common during this period and frequently resulted in fights and other forms of overt aggression (Chapter
II). Once a pair had selected a nest site, they initiated nest building, further sexual activities and territorial defense. Pairs commonly changed nest sites several times during the early part of the breeding season before settling on one location.

Egg-laying usually began in September or October and was followed by a five week incubation period during which the male and female shared incubation, changing over every few days. Little blue penguins on Banks Peninsula and Motunau Island typically laid two-egg clutches. The frequency of aggressive interactions during the egg-laying period and incubation were noticeably reduced in comparison to the pre-egg laying period. Following hatching, the adults guarded chicks for 10-25 days and changed guard duty nightly. Aggressive interactions became more common during this period, before decreasing again during the post-guard stage. During the post-guard stage, adults only returned to feed chicks during the evenings, with visits becoming less frequent toward the time chicks fledged (50-55 days).

From about 30-35 days of age, the chicks in cave colonies commonly moved about the colony, interacting with non-sibling chicks and sometimes forming small creches of three to six birds. Cave chicks were frequently involved in aggressive interactions with non-parent adults, particularly unmated club birds and adults at neighbouring nests. In burrow habitats, chicks rarely creched, and they usually interacted with parents and siblings only. During the daytime, cave adults and chicks freely moved around within the cave, although most social interactions occurred at night. In burrow habitats, neither adults nor chicks moved from their nest sites during the daytime and only rarely at night.

After the chicks fledged (late December to February), breeding pairs abandoned breeding sites and remained at sea for several weeks, presumably to replenish fat supplies before the moult. In burrow colonies, moulting adults tended to remain solitary throughout the two to three week moulting period. In cave colonies, moulters gathered in small groups and interacted frequently with other moulting adults and late fledging chicks. Once the moult was completed, the penguins returned to the sea and rarely came ashore again until the beginning of the next breeding season.
Chapter I

Intraspecific variation in social repertoires: evidence from cave- and burrow-dwelling little blue penguins

Intraspecific variation in life history (e.g. Dobson & Murie 1987; Groeters & Dingle 1987), mating systems (e.g. Sacher 1986; see Lott 1984 for a review), and morphology (e.g. Levins 1968; Lloyd 1984; Lively 1986) is commonly associated with environmental heterogeneity. Despite behaviour being considered the most flexible and inexpensively modified component of phenotype (Parker 1982), I have been unable to find any literature on intraspecific variation in social repertoires associated with environmental heterogeneity (but see Fagen 1987). Ethologists have traditionally viewed social repertoires as static and invariable across localities, and as a consequence, researchers have tended to study a single group or population, and then generalize their findings. Variation was ignored or considered aberrant.

Recently, however, this view has been challenged (e.g. Hinde & Stevenson-Hinde 1976; Dunbar 1982; Caro & Bateson 1986). Social systems are more correctly seen as the dynamic consequence of a complex and ever changing interaction between biotic and abiotic conditions. Investigation of the results of social flexibility, whether advantageous, disadvantageous or neutral, and the processes initiating variability are a key to understanding the nature of social systems and their evolution (Dunbar 1982). In the present study I report that little blue penguins, Eudyptula minor, sole members of the genus Eudyptula, do not possess a single 'fixed' repertoire of social behaviour. The results suggest, rather, a general 'social predisposition' (Mason 1978), which provides a flexible basis from which more than one social outcome can be generated. Intraspecific variation in social outcomes, apparent in little blue penguin agonistic repertoires, is correlated with environmental heterogeneity.

Little blue penguins are nocturnally active on land and occupy a wide range of nesting habitats along the coastlines of New Zealand and Australia. I examined the agonistic behaviour of this species in two contrasting nesting habitats: caves and burrows. In caves, males form advertising clubs (3-6 individuals) to attract females; breeding pairs nest in tight colonial aggregations (nests c. 1-2 m apart); and conspecifics have little or no physical barriers separating them. In burrows, males
advertise solitarily for mates along shore lines; breeding pairs nest solitarily or in semi-colonial conditions (nests c. 2-5 m or more apart); and conspecifics are physically isolated from one another. The lack of a simple 'species-typical environment' (Bekoff 1978a; Boorman & Levitt 1980) in little blue penguins makes this species an ideal subject for the study of intraspecific variability in social behaviour associated with environmental heterogeneity.

The main objectives of this paper are: (1) to quantify and compare the form and context of agonistic behaviour used by cave- and burrow-dwelling little blue penguins; (2) to provide the first detailed analysis of agonistic behaviour in little blue penguins, one of the least known species/genera in the penguin family; (3) to describe how intraspecific variation in little blue penguin social behaviour may develop; and (4) to provide an explanation for why intraspecific variation may be maintained.

METHODS

Two hundred hours (c. 150 h from cave dwellers; 50 h from burrow dwellers) of focal animal observations (Altmann 1974) were obtained from two cave and two burrow populations of little blue penguins over three breeding seasons (June-February 1984-1987). Observations, conducted twice weekly, were distributed equally within each breeding season. The two cave populations and one of the burrow populations were situated on Banks Peninsula, South Island, New Zealand. The second burrow population was located on Motunau Island, 30 km north of Banks Peninsula and 1.5 km off the east coast. Ad libitum samples were collected from seven other little blue penguin colonies around the New Zealand mainland and offshore islands, the Chatham Islands and Australia.

Focal animal samples were obtained from males and females defending nest sites (i.e. territorials) at six burrow nest sites and 29 cave nest sites. Focal animal observations were also obtained from unmated males and females (i.e. non-territorials) occupying central 'common' areas (areas without nest sites) of caves. Non-territorial males in caves formed small calling clubs in common areas (usually on small mounds or hills) to attract non-territorial females. Non-territorial males in burrow colonies tended to call solitarily from spaces beneath rocks and dense vegetation along the shoreline, attracting non-territorial females. Because the location of non-territorials in burrow colonies made them impossible to sample using focal animal techniques, ad libitum samples were obtained whenever
possible. All statistical analyses were, therefore, based on four focal animal classes in caves (i.e. territorial males, territorial females, non-territorial males and non-territorial females) and two focal animal classes in burrows (i.e. territorial males and territorial females).

In caves, focal animal observation periods (i.e. sessions) \((N=398)\) were 20-25 min long. In burrows, focal animal sessions \((N=55)\) were 50-55 min long. Focal individuals in both caves and burrows were marked with numbered metal flipper bands or were recognized by distinctive patterns on their flippers. Sex of individuals was determined by noting position during a minimum of three copulations, since reverse copulation has been observed in other penguin species (e.g. Richdale 1941). Penguins were not handled following banding. To avoid sexual bias and to minimize interference, band-readings (to determine the sex and identity of the focal individual) were made at the end of observation sessions.

All observations were made using a Zeniscope Night Vision System (Model NVC-100) in conjunction with a National Panasonic video recorder (Model WV100) and camera (Model WVP100N) or a Sony audio recorder (Model TC-D5M). Permanent observation boxes were constructed over the nest bowl of five burrow nests. The sides of each box were painted flat black to reduce the reflection of light. A square of transparent Perspex at the base of each box replaced the burrow roof. The upper lid of each box was hinged and had a mirror mounted on the lower surface. When in use, the lid was raised and angled such that the image of the burrow occupants was reflected down a 2 m black fabric tube attached to the side of the box. The night vision equipment and recorder were mounted at the other end of the fabric tube. Ten min was allowed for the animals to settle between gear set-up and the initiation of observations.

In caves, the night vision equipment and recorder were set up 4 m away from subjects. A hide was not necessary, due to low ambient light. Where possible, the equipment was set up behind rocks or driftwood to minimize disturbance. In both cave and burrow situations, a light emitting diode or low-watt torch bulb wrapped in red Cellophane and connected to a penlight battery provided ample light for recording through the night vision equipment.

In caves, a Nakamichi microphone (Model CM300) with a shot-gun head (Model CP-4) was mounted next to the night-vision equipment to record acoustic behaviour at the nest. In burrows, the Nakamichi microphone with a non-directional head (Model CP-1) was mounted to the Perspex roof at the base of observation boxes. Acoustic behaviour, recorded on the audio track
of the video recorder or one channel of the Sony recorder, was analysed on a Kay 6061-B Sonograph. Sonograms were produced using the 80-8000 Hz or 160-16000 Hz scale (linear setting) using the wide band pass filter.

For each session on a given focal animal, I collected the following data: (1) the agonistic interaction rate (interactions per min), (2) the types of agonistic behaviour and the proportion of interactions involving each (proportion per interaction), (3) the mean length of each agonistic behaviour (sec), (4) the distance away from the opponent when each agonistic behaviour was initiated (m), (5) the vocal component and characteristics of vocal accompaniment (proportion of times each vocal type is used with each agonistic behaviour), and, if the focal animal was with a partner, (6) the proportion of intrusions that the male and female partner responded to. The mean values, for all six measures, were calculated for each session on a given focal animal. Session means for each measure were then averaged over all sessions for each focal animal (range 1-28) to obtain 'total means' for each individual.

The total means for each individual were used for analysis. Individuals were grouped into the four focal animal classes for caves and the two focal animal classes for burrows. Since all comparisons are based on individual means, N is always equal to the number of individuals in each focal animal class (i.e. Cave: territorial males N=29, territorial females N=29, non-territorial males N=13, non-territorial females N=13; Burrow: territorial males N=6, territorial females N=6). Within and between habitat variation among classes was tested in the following ways:

(1) Differences in the agonistic interaction rate between habitats were tested using a two sample t-test. Only territorials (males and females lumped) were compared across habitats since no focal animal samples could be obtained from non-territorial burrow subjects.

(2) Differences among cave focal animal classes in the proportion of interactions where a given agonistic behaviour was used were tested using a one-way ANOVA and a Duncan’s multiple-range test (=Dmrt). Differences between the two burrow classes were tested using a paired t-test. Differences among cave and burrow territorial classes in the proportion of interactions where equivalent behaviour patterns were used were tested using a one-way ANOVA and Dmrt or, where appropriate, a two sample t-test.

(3) Differences among cave focal animal classes in the length of agonistic behaviours were tested using a one-way ANOVA and Dmrt. Differences between burrow focal animal classes in the length of agonistic behaviour were tested using paired t-tests. Differences among cave and
burrow territorials in the length of equivalent behaviour patterns was tested using a one-way ANOVA and Dmrt.

(4) The proportion of interactions at each of four standardized distances (i.e. <1 m, 1-2 m, 2-3 m, and >3 m) in which each agonistic behaviour occurred was determined for territorials in both habitats using a two-way ANOVA without replication and Dmrt.

(5) The presence or absence of vocalizations and the proportion of each type of vocalization used with each agonistic behaviour were recorded, but not tested statistically.

(6) The proportion of intrusions that territorial males and females in each habitat reacted to was compared using paired t-tests.

Proportional data were arcsin transformed before statistical tests were conducted. Parametric tests were used for all analyses so that specific comparisons could be made between batches tested using ANOVA and Dmrt. The distribution of data used in each one-way or two-way ANOVA was assessed for normality. Violations of the assumption of normality were not common and, when they did occur, were rarely severe.

For each agonistic behaviour I provide details on: (1) Actors (note that actor classes included in brackets are from ad libitum samples [N > 5 for each] and were not included in the analyses), (2) Form (including posture, vocal components and duration), and (3) Performance (including proportion of interactions in which the behaviour was used, variation between focal animal classes, and distance from the opponent when the behaviour was initiated).

**Egg Transfer Experiment**

To estimate the degree to which inter-habitat variation in the size and form of agonistic repertoires was genetically mediated, I transferred 44 first-laid eggs between habitats (i.e. 22 first eggs from cave nests were swapped with 22 first eggs from burrows). All swaps were completed before the second egg of each clutch was laid. The transfers were conducted in September or October 1985.

I began each swap by replacing the single first egg of an incubating parent with a warmed "dummy" egg (i.e. a medium sized chicken egg). The dummy egg was immediately accepted and incubated by the parent in all cases. The removed penguin egg was then placed in an insulated pocket next to my skin and transported to the second habitat within 2-3 hours.

The egg from the first habitat was then marked with a water resistant pen and traded for the egg of a foster parent in the second habitat. The foster parent's egg was similarly marked and then transported to the first habitat.
where it replaced the dummy egg. I found that the dummy egg was always warm on my return to the first habitat, indicating that it was being incubated by the parent. Approximately one half of the transfers were initiated from cave habitats and half from burrows.

At hatching, transferred chicks and their foster siblings were marked with adjustable leg rings until their flippers were large enough to hold regular flipper bands. During the two weeks prior to fledging (i.e. estimated by hatching date), focal animal techniques were used to record the occurrence and frequency of agonistic behaviours used by transferred and locally bred chicks in the cave habitat. Approximately 8 ten minute focal animal sessions were conducted on each chick.

I restricted my analysis to chicks from clutches where both young survived to fledge and to chicks from which I had obtained observations of at least 25 agonistic interactions. As a result of these restrictions, my sample size was reduced to three transferred chicks that had been raised with a local chick, three local chicks that had been raised with a transferred chick and four local chicks that had been raised with their natural sibling.

It was not possible to use focal animal techniques to obtain data on chick behaviour in the burrow habitat since both locally bred and transferred chicks spent most of their time within the burrow (i.e. out of sight). However, ad libitum observations of one or two agonistic interactions were obtained from each of four transferred chicks and three local chicks in the burrow habitat. Ad libitum samples were obtained during the two weeks prior to fledging.

RESULTS

Little blue penguins had an extensive repertoire of agonistic behaviour. My findings are summarized at the end of the Results section in Table I. Cave-dwelling little blue penguins used 22 distinct agonistic behaviours (including 54 variations based primarily on differences in vocal accompaniment for each agonistic behaviour); burrow-dwellers used 13 (including 29 variations). The agonistic interaction rate for territorial cave-dwellers (average of 0.34 interactions per min) was approximately three times that for territorial burrow-dwellers (average of 0.10 interactions per min). The difference was highly significant (two sample t-test, $P < 0.001$). When both partners were present at cave nest sites, males were involved in a significantly higher proportion of interactions.
(85.8%) than females (59.9%) (paired t-test, \( P < 0.001 \)). In burrow populations, males were also involved in a higher proportion of interactions (91.1%) than females (55.0%) but the difference was not significant (paired t-test, NS).

I distinguish between three main categories of agonistic behaviour: (1) defensive behaviour; (2) offensive behaviour; and (3) overt aggression. Following the habitat specific descriptions of behaviour used in each category, I compare equivalent agonistic behaviours between the two habitats. Figures 1 and 2 show vocal components used in conjunction with agonistic displays. The vocal components are typical of little blue penguins inhabiting Banks Peninsula and Motunau Island.

![GROWL](image1)

![LOW BRAY](image2)

![MEDIUM BRAY](image3)

![FULL BRAY](image4)

**Figure 1. Growl and Braying vocalizations used by little blue penguins during agonistic interactions. Examples of each vocalization are from different individuals.**

**Defensive Behaviour**

Defensive behaviours were those that made actors cryptic, facilitated their ability to avoid interaction, and hid vulnerable segments of the body (i.e. head, eyes) from the opponent. The defensive behaviour category could be split into two sub-categories: (a) stationary behaviour (cave: Indirect Look and Face Away; burrow: Face Away); and (b) distance increasing behaviour (cave: Submissive Hunch and Low Walking; burrow: Low Walking). Fig. 3 shows the defensive behaviours used by little blue
Figure 2. Hiss, Aggressive Bark and Aggressive Yell vocalizations used by little blue penguins during agonistic interactions. Examples of each vocalization are from different individuals with the exception of Hiss. The unlabelled Hiss is from a different individual.
penguins. Fig. 4 shows histograms of the proportions of interactions, at four interaction distances, in which each defensive behaviour was used by little blue penguins (territorials only).

**Cave habitats**

(1) *Indirect Look*

**Actors:** Territorial males and females, non-territorial males and females.

**Form:** Actors Indirect Look by turning the bill and sometimes the body 45° away from the opponent while stationary. The actor looked obliquely to the opponent (Fig. 3). Only territorial females used a vocalization during Indirect Look. Territorial females used Growl (Fig. 1) with 7.6% of Indirect Looks. Indirect Look was performed for an average of 8.0 s before changing behaviours. There were no differences between cave focal animals in the length of the behaviour (one-way ANOVA, NS).

**Performance:** Birds used Indirect Look in 7.3% of interactions. There was no significant difference among cave focal animals in the proportion of interactions in which the behaviour was performed (one-way ANOVA, NS). Indirect Look was performed most frequently at lower interaction distances (Dmrt, \( P < 0.01 \); Fig. 4).

(2) *Face Away*

**Actors:** Territorial males and females, non-territorial males and females.

**Form:** Actors Faced Away silently with the body turned directly away from the opponent and flippers held to the sides while stationary (Fig. 3). The actor turned its head to one side and looked to the opponent obliquely. Focal animals Faced Away for an average of 7.7 s before changing behaviour. There were no differences between cave classes in the length of Face Away (one-way ANOVA, N.S.).

**Performance:** Birds used Face Away in 6.9% of interactions. There was no significant difference between cave classes in the proportion of interactions in which Face Away was performed (one-way ANOVA, NS). Face Away was performed most frequently at lower interaction distances (Dmrt, \( P < 0.05 \); Fig. 4).

(3) *Low Walking*

**Actors:** Territorial males and females, non-territorial males and females.

**Form:** Actors Low Walked silently, with the body held low to the ground. The flippers were held to the sides as the bird walked (in 49.0% of cases) or ran (in 51.0% of cases) past or away from the opponent (Fig. 3). Pairs Low Walked in 'single file'. During interactions, focal animals Low Walked for an average of 5.5 s before changing behaviour. There were no within-habitat differences between classes of cave animals in the duration
Figure 3. Defensive behaviour used by little blue penguins during agonistic interactions. Cave-dwellers used all four behaviours; burrow-dwellers used only Low Walk and Face Away. Compare Figure 3 to Figure 4.

of Low Walking (one-way ANOVA, NS).

Performance: Cave animals used Low Walk in 6.0% of interactions. There was no significant difference between cave focal animal classes in the proportion of interactions in which Low Walk was performed (one-way ANOVA, NS). Low Walking was performed equally at all four interaction distances (two-way ANOVA, NS; Fig. 4). Low Walking was the normal mode of movement whenever individuals moved through areas where territories were defended.

(4) Submissive Hunch

Actors: Territorial males, non-territorial males (territorial females and non-territorial females).

Form: Actors Submissive Hunched silently with the head lowered and stretched away from the opponent (Fig. 3). The actor took a few steps away from the opponent while in Submissive Hunch and then stopped. Focal animals performed Submissive Hunch for an average of 3.6 s before changing behaviour. There was no difference between territorial and non-territorial males in the length of Submissive Hunch (two sample t-test, NS).

Performance: Males used Submissive Hunch in 1.5% of interactions. There was no significant difference between territorial and non-territorial males in the proportion of interactions in which Submissive Hunch was used (two sample t-test, NS). Submissive Hunch was performed most frequently at
Figure 4. Performance distance profiles for defensive behaviour. Histograms show the proportion of interactions, at each of four standard distances, in which each behaviour was used. Probability values indicate the significance or non-significance (NS) of variation between the proportion of interactions at the four distances that male or female territorials used each behaviour (two-way ANOVA). Bars with the same letter(s) are not significantly different from one another. Bars not sharing any letter are significantly different (P < 0.05; Dmrt).

lower interaction distances (Dmrt, P < 0.01; Fig. 4).

Burrow habitats

(1) Face Away

Actors: Territorial females (non-territorial males and females).

Form: Actors Faced Away silently with the body turned to the rear of the burrow while looking back to the burrow entrance with the head lowered
Territorial females Faced Away for an average of 14.2 s before changing behaviour.

**Performance:** Territorial females Faced Away in 40.6% of interactions. Females used Face Away most frequently at lower interaction distances (Dmrt, $P < 0.05$; Fig. 4).

(2) **Low Walking**

**Actors:** Territorial males and females (non-territorial males and females).

**Form:** Actors Low Walked silently with the body held low to the ground (Fig. 3). The flippers were held to the sides as the bird walked (50.0% of cases) or ran (50.0% of cases) past or away from the opponent. Pairs Low Walked in single file. During interactions, burrow focal animals Low Walked for an average of 4.0 s before changing behaviour. There was no significant difference between territorial males and females in the length of Low Walk (Paired t-test, NS).

**Performance:** Birds used Low Walk in 2.8% of interactions. There was no significant difference between territorial males and females in the proportion of interactions in which Low Walking was used (paired t-test, NS). Low Walk was used equally at all interaction distances (two-way ANOVA, NS; Fig. 4). Low Walking was the normal mode of moving from the sea up pathways leading to burrows, especially when passing other burrow entrances along the way.

**Cave vs. burrow: defensive behaviour**

Cave-dwelling little blue penguins used four defensive behaviour patterns (stationary behaviours: Indirect Look and Face Away; distance increasing behaviours: Submissive Hunch and Low Walking); burrow-dwelling little blue penguins used two (stationary behaviour: Face Away; distance increasing behaviour: Low Walking) (Fig. 3). Low Walking and Face Away were identical between habitats; there were no burrow equivalents to the cave behaviours Indirect Look or Submissive Hunch.

(1) **Face Away**

Face Away was identical in form between habitats (Fig. 3). In both habitats, the behaviour was performed silently. In burrow habitats, the behaviour was used by females only. In cave habitats, both males and females used the behaviour. There was no significant difference in the length of the display between habitats (cave: females 15.2 s, males 10.6 s; burrow: females 14.2 s) (one-way ANOVA, NS). However, burrow females used the behaviour in a significantly higher proportion of interactions than either male or female cave dwellers (cave: females 6.2%, males 3.0%; burrow: females 40.6%) (Dmrt, $P < 0.001$). In both habitats, Face Away
tended to be used more frequently at < 1 m and 1-2 m than at other interaction distances ($P < 0.05$; Fig. 4).

(2) Low Walking

Low Walking was identical in form between habitats (Fig. 3). In both habitats, the behaviour was performed silently. Also, in both habitats, 'Walk' was replaced by 'Run' in c. 50% of interactions. There was no significant difference in the length (cave 5.9 s; burrow 4.0 s) or in the proportion of interactions (cave 2.6%; burrow 2.8%) in which Low Walking was used by territorials between habitats (one-way ANOVA, NS). Low Walking was performed equally at all interaction distances in both habitats (two-way ANOVA, NS) (Fig. 4).

Offensive Behaviour

Offensive behaviours were those that made actors obvious, reduced their chances of escape, and/or exposed vulnerable sections of their body (i.e. eyes, head) to their opponent. The offensive behaviour category was split into three sub-categories: (a) stationary behaviour; (b) distance reducing behaviour; and (c) contact behaviour.

(a) Stationary Behaviour

Stationary behaviour made the actor's presence and position obvious, and it involved directing the body and bill toward the opponent. Stationary behaviour never involved approaching an opponent or contact with the opponent. Fig. 5 shows postures used during these behaviours; Fig. 6 shows the proportion of interactions, at the four standardized distances, in which each stationary behaviour was used.

Cave habitats
(1) Direct Look

Actors: Territorial males and females, non-territorial males and females.

Form: The body and bill were oriented toward the opponent while stationary in a lying or standing posture (Fig. 5). The behaviour was most commonly performed silently, but territorial males and females used Growl in 2.2% of Direct Looks (Fig. 1). Non-territorials were not observed using a vocal component during Direct Look. Direct Look was performed for an average of 10.9 s before changing behaviour. There was no significant difference between classes of cave birds in the length of Direct Look (one-way ANOVA, NS).

Performance: Birds used Direct Look in 70.2% of interactions. There was no significant difference in the proportion of interactions in which Direct Look was performed by different classes of cave focal animals (one-way ANOVA, NS). Direct Look was performed most frequently at higher
Fig. 5. Stationary behaviour used by cave- and burrow-dwellers during offense. Solid curved lines from the bill indicate that the behaviour always had a vocal component. Dashed curved lines from the bill indicate that the behaviour was used silently or with a vocalization. Compare Fig. 5 to Fig. 6.
Figure 6. Performance distance profiles for stationary offensive behaviour. Histograms show the proportion of interactions, at each of four standard distances, in which each behaviour was used. Probability values indicate the significance or non-significance (NS) of variation between the proportion of interactions at the four distances that male or female territorials used each behaviour (two-way ANOVA). Bars with the same letter(s) are not significantly different from one another. Bars not sharing any letter are significantly different ($P < 0.05$; Dmrt).
interaction distances (Dmrt, $P < 0.001$; Fig. 6).

(2) **Point**

**Actors:** Territorial males and females, non-territorial males and females.

**Form:** The body was held stationary and low to the ground with the neck and flippers outstretched (Fig. 5). The actor's bill 'tracked' the opponents movement. Territorials usually performed Point silently, but accompanied the behaviour with Growl in 13.9% of cases (Fig. 1). Non-territorials were not observed using a vocal component in conjunction with Point. Point was given for an average of 11.7 s before changing behaviours. There was no significant difference between classes of cave focal animals in the length of Point (one-way ANOVA, NS).

**Performance:** Birds used Point in 14.7% of interactions. There was no significant difference between classes of cave focal animals in the proportion of interactions in which Point was used (one-way ANOVA, NS). Point was performed most frequently at middle (1-2 m to 2-3 m) interaction distances (Dmrt, $P < 0.01$; Fig. 6).

(3) **Directed Flipper Spread**

**Actors:** Territorial males and females, non-territorial males and females.

**Form:** Actors Directed Flipper Spread by standing erect with flippers outstretched (Fig. 5). The actor's bill and body was oriented toward the intruder. Directed Flipper Spread was performed silently (64.6% of cases), with Growl (12.1% of cases), with Low Bray (11.8% of cases), with Medium Bray (6.6% of cases) and with Full Bray (4.9% of cases) (Fig. 1). Directed Flipper Spread averaged 9.3 s in duration. There was no significant difference between classes of cave animals in the length of Directed Flipper Spread (one-way ANOVA, NS).

**Performance:** Birds used Directed Flipper Spread in 11.8% of interactions. There was no significant difference between classes of cave focal animals in the proportion of interactions in which Directed Flipper Spread was used (one-way ANOVA, NS). Directed Flipper Spread was performed most frequently at intermediate (1-2 m to 2-3 m) interaction distances (Dmrt, $P < 0.01$; Fig. 6).

(4) **Bowed Flipper Spread**

**Actors:** Territorial males and territorial females.

**Form:** Bowed Flipper Spread was performed with flippers out-stretched and the head bowed so that the bill pointed into the nest bowl (Fig. 5). Actors turned in small circles in the nest while performing Bowed Flipper spread. The behaviour was always accompanied by a vocal component. Territorials Bowed Flipper Spread using Growl (49.7% of cases), Low Bray
(17.1% of cases), Medium Bray (17.6% of cases), and Full Bray (15.6% of cases) (Fig. 1). Bowed Flipper Spread was performed for an average of 11.7 s before changing behaviours. There was no significant difference between territorial males and females in the duration of Bowed Flipper Spread (paired t-test, NS).

**Performance:** Bowed Flipper Spread was most commonly performed following physical interactions or the chasing of an opponent away from the nest. Territorial males used Bowed Flipper Spread significantly more often during interactions than did territorial females (paired t-test, $P < 0.05$). Males used Bowed Flipper spread in 1.9% of interactions. Females used Bowed Flipper spread in only 0.6% of interactions. Bowed Flipper Spread was performed equally at all interaction distances (two-way ANOVA, NS; but see Fig. 6).

(5) Directed Mutual Display

**Actors:** Territorial pairs, non-territorial pairs.

**Form:** Partners stood erect with flippers out-stretched (interlocked or resting on the partners back) and directed their bodies and bills toward the intruder. The posture adopted was similar to that of the Directed Flipper Spread (Fig. 5). Directed Mutual Display always had a vocal component. The vocalizations of the male and female during mutual displays were not different from the braying vocalizations of solo displays; the male and female simply overlapped vocal contributions with no apparent temporal synchrony. Vocal components include: Growl (5.7% of cases); Low Bray (39.3% of cases); Medium Bray (36.9% of cases); and Full Bray (18.1% of cases) (Fig. 1). There was no significant difference in the length of Directed Mutual Display between territorial and non-territorial pairs (two sample t-test, NS). Directed Mutual Display was performed for an average of 11.0 s before changing behaviour.

**Performance:** Directed Mutual Display was initiated by either the male or female. Non-territorials used Directed Mutual Display in 16.5% of interactions, a significantly greater proportion of interactions than that of territorials (8.5% of interactions) (two sample t-test, $P < 0.05$). Directed Mutual Display was not performed equally over all interaction distances (Dmrt, $P < 0.05$). Directed Mutual Display was performed significantly more often at > 3 m and 2-3 m than at <1m ($P < 0.05$) but not significantly more than at 1-2 m.

(6) Bowed Mutual Display

**Actors:** Territorial pairs.

**Form:** The pair stood erect but bowed their heads so that the bills pointed into the nest bowl. The bills would sometimes vibrate horizontally. The
posture adopted was similar to that used in the Bowed Flipper Spread (Fig. 4). Both patted each other on the back or sides with out-stretched flippers and circled the nest site. The behaviour was always accompanied by a vocal component. Vocal components included: Growl (5.0% of cases); Low Bray (61.8% of cases); Medium Bray (20.3% of cases); and Full Bray (12.9% of cases) (Fig. 1). Bowed Mutual Display was performed for an average of 12.1 s before changing behaviours.

**Performance:** Bowed Mutual Display was initiated by either the male or female. The behaviour was used in 13.7% of interactions involving territorial pairs. Bowed Mutual Display was not performed equally at all interaction distances (Dmrt, $P < 0.001$). The behaviour was performed significantly more often at > 3 m and 2-3 m than at <1 m or 1-2 m ($P < 0.05$).

(7) **Upward Mutual Display**

**Actors:** Territorial pairs.

**Form:** The pair stood erect next to one another but not in contact and vocalized upward with flippers out-stretched. Vocal components included: Growl (0.5% of cases); Low Bray (56.3% of cases); Medium Bray (26.4% of cases); and Full Bray (16.8% of cases) (Fig. 1). Pairs performed Upward Mutual Display for an average of 13.8 s before changing behaviours.

**Performance:** Either males or females initiated Upward Mutual Display. The behaviour was used in 7.0% of interactions involving territorial pairs. Upward Mutual Display was not performed equally at all interaction distances (Dmrt, $P < 0.001$). The behaviour was performed significantly more often at > 3 m and 2-3 m than at <1 m and 1-2 m ($P < 0.05$).

**Burrow habitats**

(1) **Stretch-neck Look**

**Actors:** Territorial males and females (non-territorial males and females).

**Form:** The actor's flippers were held to the sides of its body while the neck was stretched such that the bill and part of the head protruded from the burrow entrance (Fig. 5). The behaviour was usually performed silently but in 2.1% of cases was performed with the Growl vocalization (Fig. 1). Stretch-neck Look was given for an average of 13.3 s before changing behaviours. There was no significant difference between males and females in the length of Stretch-neck Look (paired t-test, NS).

**Performance:** Stretch-neck Look was used in 64.9% of interactions. There was no significant difference in the proportion of interactions in which males and females used Stretch-neck Look (paired t-test, NS). Stretch-neck Look was performed most frequently at higher interaction distances (Dmrt, $P < 0.001$; Fig. 6).
(2) Bill Vibe

**Actors:** Territorial males and females.

**Form:** The actor held its body low with the bill pointing to the entrance (Fig. 5). The bill was vibrated horizontally while the actor Growled (81.8% of cases) (Fig. 1) or looked silently (18.2% of cases). Bill Vibe was given for an average of 12.0 s before changing behaviours. There was no significant difference between males and females in the duration of Bill Vibe (paired t-test, NS).

**Performance:** Burrow males used Bill Vibe in significantly more interactions than burrow females (paired t-test, \( P < 0.05 \)). Burrow males used Bill Vibe in 24.2% of interactions. Females used Bill Vibe in only 4.6% of interactions. Bill Vibe was performed most frequently at middle (1-2 m to 2-3 m) interaction distances (Dmrt, \( P < 0.05 \); Fig. 6).

(3) Directed Flipper Spread

**Actors:** Territorial males and females.

**Form:** The actor's body was stretched low with the head directed toward the entrance and flippers raised (Fig. 5). Actors used the Low Bray (67.7% of cases) or Medium Bray (33.3% of cases) vocalizations during Directed Flipper Spread (Fig. 1). Actors used Directed Flipper Spread for an average of 7.2 s before changing behaviours. There was no significant difference between males and females in the duration of Directed Flipper Spread (paired t-test, NS).

**Performance:** Directed Flipper Spread was used in 2.5% of interactions. There was no significant difference in the proportion of interactions in which males and females performed Directed Flipper Spread (paired t-test, NS). Directed Flipper Spread was used most frequently at middle to higher interaction distances (Dmrt, \( P < 0.05 \); Fig. 6).

(4) Bowed Flipper Spread

**Actors:** Territorial males and females.

**Form:** The head was bowed so that the bill pointed into the nest bowl. The flippers were raised and the bird stepped from side to side while vocalizing (Fig. 5). In all cases the Low Bray vocalization (Fig. 1) was used in conjunction with Bowed Flipper Spread. Bowed Flipper Spread was performed for an average of 4.7 s before changing behaviour. There was no significant difference between males and females in the length of Bowed Flipper Spread (paired t-test, NS).

**Performance:** Bowed Flipper Spread was used in 0.3% of interactions. There was no significant difference between males and females in the proportion of interactions in which Bowed Flipper Spread was used (paired t-test, NS).
Bowed Flipper Spread was performed equally at all interaction distances (two-way ANOVA, NS; but see Fig. 6).

(5) Directed Mutual Display

**Actors:** Territorial pairs (non-territorial pairs).

**Form:** The pair directed their bills toward the burrow entrance with flippers out-stretched (interlocked or resting on the partner's back). The posture was similar to that adopted in Directed Flipper Spread (Fig. 5). They vocalized while vibrating their bills horizontally. The vocalizations of the male and female during Mutual Displays were no different from the braying vocalizations of solo displays; the male and female simply overlapped vocal contributions with no apparent temporal synchrony. Vocal components included: Low Bray (38.5% of cases); Medium Bray (33.3% of cases); and Full Bray (28.2% of cases) (Fig. 1). The pair performed Directed Mutual Display for an average of 9.2 s before changing behaviour.

**Performance:** Either the male or female initiated Directed Mutual Display. The behaviour was used in 5.7% of interactions involving territorial pairs. Directed Mutual Display was not performed equally at all interaction distances (Dmrt, \( P < 0.05 \)). The behaviour was performed significantly more often at 2-3 m than at < 1 m or 1-2 m (\( P < 0.05 \)) but not significantly more often than at > 3 m.

(6) Bowed Mutual Display

**Actors:** Territorial pairs.

**Form:** The pair bowed their heads and bodies low so that their bills pointed into the nest bowl. The bills vibrated from side to side as the pair tapped one another's backs with out-stretched flippers. The posture adopted was similar to that during Bowed Flipper Spread (Fig. 5). The behaviour always had a vocal component. Vocal components used were: Growl (2.8% of cases); Low Bray (66.6% of cases); Medium Bray (24.8% of cases); or Full Bray (7.2% of cases) (Fig. 1). Bowed Mutual Display was performed for an average of 7.4 s before changing behaviour.

**Performance:** Bowed Mutual Display was initiated by either male or female. The behaviour was used in 16.9% of interactions involving territorial pairs. Bowed Mutual Display was performed equally at all interaction distances (two-way ANOVA, NS).

**Cave vs. burrow: offensive stationary behaviour**

Cave-dwelling little blue penguins used seven stationary behaviours (including three mutual displays); burrow-dwellers used six (including two mutual displays). The cave behaviours Direct Look, Point, Directed Flipper Spread, Bowed Flipper Spread, Directed Mutual Display and Bowed Mutual
Display corresponded closely with the burrow behaviours Stretch-neck Look, Bill Vibe, Directed Flipper Spread, Bowed Flipper Spread, Directed Mutual Display and Bowed Mutual Display, respectively (Fig. 5). There was no burrow equivalent to the cave behaviour Upward Mutual Display.

1) Direct Look / Stretch-neck Look

These two behaviour patterns were similar in form (Fig. 5) and context. Both were performed silently in most cases but were sometimes accompanied by the Growl vocalization (cave 2.2%; burrow 2.1%) (Fig. 1). There was no significant difference between the displays of territorials in length (cave 12.7 s; burrow 13.3 s) or in the proportion of interactions in which the behaviours were used (cave 63.8%; burrow 64.9%) (one-way ANOVA, NS). The behaviours were the most common offensive behaviours in their respective habitats and were performed equally by males and females. Both behaviours tended to be used more at 2-3 m and > 3 m than at lower interaction distances (Fig. 6).

2) Point / Bill Vibe

These two behaviour patterns were similar in form (Fig. 5) and context. Both were performed either silently or with Growl (cave 13.9%; burrow 31.8%) (Fig. 1). There was no significant difference between the behaviours of territorials in length (cave 13.5 s; burrow 12.0 s) or in the proportion of interactions involving the behaviours (cave 12.9%; burrow 14.4%) (one-way ANOVA, NS; but note that a paired t-test showed that male burrow dwellers used Bill Vibe significantly more than females). The behaviours were the second most common offensive behaviours in their respective habitats. Both behaviours tended to be used more at 1-2 m and 2-3 m than at lower or higher interaction distances (Fig. 6).

3) Directed Flipper Spread

The cave and burrow examples of this behaviour were virtually identical and therefore given the same name. In both habitats the behaviour was accompanied by one of the Braying vocalizations (Fig. 1) but in caves the behaviour was also frequently performed silently (64.6%). There was no significant difference between habitats in the behaviour's length (cave 9.3 s; burrow 7.2 s) or in the proportion of interactions in which the behaviour was used (cave 8.6%; burrow 2.5%) (one-way ANOVA, NS). In both habitats the behaviour was used most at distances of > 1 m (Fig. 6).

4) Bowed Flipper Spread

The cave and burrow examples of this behaviour were virtually identical and therefore given the same name. Both behaviours were always accompanied by vocal components (in caves, Growl and Braying; in burrows, Low Brays
only) (Fig. 1). There was no significant difference between habitats in the behaviour's length (cave 11.7 s; burrow 4.7 s) (one-way ANOVA, NS). Cave males performed the behaviour more frequently than cave females and burrow dwellers (cave males 1.9%; cave females 0.6%). In burrows, both males and females performed the behaviour equally (burrow males 0.4%; burrow females 0.2%). However, there was no significant overall difference between habitats in the proportion of interactions in which the behaviours were used (one-way ANOVA, NS). Both behaviours were performed equally at all interaction distances (but see Fig. 6).

(5) Directed Mutual Display

The cave and burrow examples of this behaviour were virtually identical and therefore were given the same name. Both behaviours were always accompanied by a vocal component (in caves, Growl and Braying; in burrows, Braying only) (Fig. 1). There was no significant difference between habitats in the length (cave 11.0 s; burrow 9.2 s) or in the proportion of interactions in which the display is used (caves 8.5%; burrows 5.7%) (two sample t-test, NS). In both habitats, the behaviours tended to be used at 2-3 m and > 3 m more than at lower interaction distances.

(6) Bowed Mutual Display

The cave and burrow examples of this behaviour were virtually identical and therefore were given the same name. Both behaviours were always accompanied by a vocal component (either Growl or Braying) (Fig. 1). There was no significant difference in the length (cave 12.1 s; burrow 7.4 s) or in the proportion of interactions involving the behaviours (cave 13.7%; burrow 16.9%) (two sample t-test, NS). In both habitats, the behaviours tended to be performed at 2-3 m and > 3 m more than at lower interaction distances (but in burrows the difference was not significant).

(b) Distance Reducing Behaviour

Distance Reducing Behaviour made actors obvious, involved directing the bill and body toward the opponent and reduced the distance from the opponent. Distance Reducing Behaviour never involved contact with the opponent. Fig. 7 shows postures used in Distance Reducing Behaviours. Fig. 8 shows the proportion of interactions at four distances in which each Distance Reducing Behaviour was used.

Cave habitats

(1) Zig-zag Approach

 Actors: Territorial males and females, non-territorial males and females.
 Form: Actors Zig-zag Approached by moving toward the opponent at oblique angles. At the corners of each zig-zag the actor paused, turned, and moved
forward at the opposite angle. Zig-zag Approach was performed with the body and head held low to the ground (Fig. 7). The flippers were raised away from the body during the approach. Zig-zag Approach was usually performed silently but in 4.9% of cases was performed with the Growl vocalization (Fig. 1). Zig-zag Approach was performed for an average of 6.9 s before changing behaviour. There was no significant difference between cave focal classes in the length of Zig-zag Approach (one-way ANOVA, NS).

**Performance:** Birds used Zig-zag Approach in 16.8% of interactions. There was no significant difference in the proportion of interactions in which Zig-zag Approach was used by focal classes (one-way ANOVA, NS). Zig-zag Approach was used most frequently at middle (1-2 m to 2-3 m) interaction distances (Dmrt, $P < 0.001$; Fig. 8).

(2) **Directed Flipper Spread Approach**

**Actors:** Territorial males and females, non-territorial males and females.

**Form:** Actors Directed Flipper Spread Approached by walking straight toward the intruder with bodies held erect and flippers extended (Fig. 7). The bill was directed toward the opponent. Directed Flipper Spread Approach was performed silently (88.0% of cases), with Growl (10.4% of cases), or with Low Bray (1.7% of cases) (Fig. 1). Directed Flipper Spread Approach was performed for an average of 6.7 s before changing behaviours. There was no significant difference between cave focal animal classes in the duration of Directed Flipper Spread Approach (one-way ANOVA, NS).

**Performance:** Birds used Directed Flipper Spread Approach in 9.0% of interactions. There was no significant difference between cave focal animal classes in the proportion of interactions in which Directed Flipper Spread Approach was used (one-way ANOVA, NS). Directed Flipper Spread Approach was used most frequently at lower to middle interaction distances (Dmrt, $P < 0.001$; Fig. 8).

(3) **Direct Mutual Approach**

**Actors:** Territorial pairs.

**Form:** The pair moved directly toward the intruder with flippers interlocked or touching each others' backs. The posture was similar to that adopted during Direct Flipper Spread Approach (Fig. 7). Both directed their bill at the intruder while vocalizing using Low Bray (50.0% of cases) or Full Bray (50.0% of cases) (Fig. 1). Direct Mutual Approach lasted for an average of 3.0 s.

**Performance:** Territorial pairs used Direct Mutual Approach in 0.3% of interactions. The behaviour was performed equally at $< 1$ m and 1-2 m and
never observed during the sample at > 2m.

Burrow habitats
(1) Lunge Hiss
Actors: Territorial males and females.
Form: Actors Lunge Hissed by throwing themselves toward the burrow entrance with flippers extended and with the bill held open (Fig. 7). When the head was just outside the entrance the actor Hissed (Fig. 2) before springing back into the burrow using its flippers against the entrance walls. The actor then froze with an open gape toward the entrance-way. In 33.3% of cases, the Hiss vocal component was replaced by Aggressive Bark (Fig. 2). Lunge Hiss lasted an average of 4.8 s. There was no significant difference in the length of male and female Lunge Hisses (paired t-test, NS).
Performance: Birds used Lunge Hiss in 1.6% of interactions. There was no significant difference between males and females in the proportion of interactions in which Lunge Hiss was used (paired t-test, NS). Lunge Hiss was performed most frequently at lower to middle interaction distances (Dmrt, P < 0.05; Fig. 8).
Figure 8. Performance distance profiles for distance reducing offensive behaviour. Histograms show the proportion of interactions, at each of four standard distances, in which each behaviour was used. Probability values indicate the significance or non-significance (NS) of variation between the proportion of interactions at the four distances that male or female territorials used each behaviour (two-way ANOVA). Bars with the same letter(s) are not significantly different from one another. Bars not sharing any letter are significantly different ($P < 0.05$; Dmrt).

Cave vs. burrow: distance reducing behaviour

Cave-dwelling little blue penguins used 3 distinct distance reducing behaviours (including one mutual display); burrow-dwellers used one. The cave behaviours Zig-zag Approach and Direct Flipper Spread Approach matched the burrow behaviour Lunge Hiss closely in context but not in overall form (Fig. 7). The cave display Direct Mutual Approach had no burrow equivalent.

1) Zig-zag and Direct Flipper Spread Approach / Lunge Hiss

Lunge Hiss was performed using either the Hiss or Aggressive Bark vocalization (Fig. 2). Zig-zag and Direct Flipper Spread Approach were most commonly performed silently but sometimes with Growl or Bray (Fig. 1). The three displays were significantly different in length (Lunge Hiss 4.8 s; Zig-zag 7.0 s; Direct 5.1 s) (Dmrt, $P < 0.05$; note: males and females pooled for each display). There was, however, no significant difference in the proportion of interactions in which the behaviours were used (Lunge
Hiss 1.6%; Zig-zag 6.3%, Direct 4.7% (one-way ANOVA, NS). All three behaviours tended to be performed more frequently at 1-2 m than at other interaction distances (Fig. 8).

(c) Contact Behaviour

Contact behaviour involved ‘bill to bill’ or ‘bill to body’ physical contact. Actors used contact behaviour on stationary or moving opponents. Fig. 9 shows postures associated with contact behaviour.

Cave habitats

(1) Bill to Bill

Actors: Territorial males and females, non-territorial males and females.

Form: The actor placed its bill toward the opponent’s bill while both raised and lowered their heads in a ‘bobbing’ motion (Fig. 9). Actors raised their flippers slightly when bills touched. Bill to Bill was performed silently and lasted an average of 5.0 s. There was no significant difference between focal animal classes in the duration of Bill to Bill (one-way ANOVA, NS).

Performance: Birds used Bill to Bill in 5.2% of interactions involving non-territorial males; 13.9% of interactions involving non-territorial females; 1.2% of interactions involving territorial males; and 0.4% of interactions involving territorial females (Dmrt, $P = 0.05$).

(2) Bill Slapping

Actors: Territorial males and females, non-territorial males and females.

Form: The actor stood erect with flippers held away from the body while swinging its bill horizontally and knocking the opponents bill from side to side (Fig. 9). Bill Slapping was frequently interrupted by bouts of Indirect and Direct Look. If the actor Direct Looks during these bouts the opponent Indirect Looks, and vice versa. Bill Slapping was initiated again when both gave Direct Look at the same time. Bill Slapping was performed silently and lasted an average of 3.2 s. There was no significant difference between focal animal classes in the length of Bill Slapping (one-way ANOVA, NS).

Performance: Birds Bill Slapped in 5.2% of interactions involving non-territorial males; 13.9% of interactions involving non-territorial females; 1.2% of interactions involving territorial males; and 0.5% of interactions involving territorial females (Dmrt, $P = 0.09$).

(3) Breast Butt

Actors: Territorial males and females, and non-territorial males.

Form: Actors Breast Butted silently with body erect and flippers out-stretched. The actor stepped toward and pushed against the opponent
Figure 9. Contact behaviour used by cave- and burrow-dwellers during offense.
with the breast (Fig. 9). Breast Butt was performed for an average of 4.4 s before changing behaviours. There was no significant difference between territorial males, territorial females and non-territorial males in the duration of Breast Butt (one-way ANOVA, NS).

**Performance:** There was a significant difference in the proportion of interactions in which cave focal classes performed Breast Butt (Dmrt, $P < 0.01$). Non-territorial males performed Breast Butt in 11.0% of interactions; a proportion significantly higher than that for male and female territorials (0.6% of interactions) (one-way ANOVA, $P < 0.05$).

There was no significant difference between territorial males and females in the rate of Breast Butt performance.

(4) **Bill to Back**

**Actors:** Territorial males and females, and non-territorial males.

**Form:** Bill to Back was performed silently and involved placing the closed bill onto the opponent’s lower back (Fig. 9) as the opponent escaped in Low Walk or moved away in Submissive Hunch. The actor stayed with the opponent until 1-2 m away from the starting point. Bill to Back was performed for an average of 2.8 s. There was no significant difference in the length of Bill to Back between focal classes using the behaviour (one-way ANOVA, NS).

**Performance:** There was a significant difference in the proportion of interactions in which cave focal classes performed Bill to Back (Dmrt, $P < 0.05$). Non-territorial males performed Bill to Back in 4.4% of interactions; a proportion which was significantly higher than that for male and female territorials (0.2% of interactions; $P < 0.05$). There was no significant difference between territorial males and females in the rate of Bill to Back performance.

(5) **Bill Lock Twist**

**Actors:** Territorial males and females, and non-territorial males.

**Form:** Actors Bill Lock Twisted by inter-locking open gapes with the opponent and turning the head from side to side in an attempt to throw the opponent off balance (Fig. 9). The flippers were usually out-stretched during Bill Lock Twist. The behaviour was always performed in conjunction with Growl (Fig. 1) and sometimes with Aggressive Yell (30.8% of cases) (Fig. 2). Opponents Bill Lock Twist for an average of 3.8 s before changing behaviour. There was no significant difference between cave focal classes in the duration of Bill Lock Twist (one-way ANOVA, NS).

**Performance:** Bill Lock Twist was not performed equally by all cave focal animal classes (Dmrt, $P < 0.01$). Non-territorial males performed Bill Lock Twist in 5.6% of interactions; a proportion which was significantly greater
than that of male and female territorials (0.1% of interactions) \((P < 0.05)\).

**Burrow habitats**

(1) **Lunge Peck**

**Actors:** Territorial males and females.

**Form:** Actors Lunge Pecked by leaping out of the burrow entrance toward the intruder with the bill held forward (Fig. 9). After making contact with the intruder the actor stood erect with flippers out-stretched. Lunge Peck was performed silently. Lunge Peck lasted an average of 3.0 s. There was no significant difference between males and females in the length of Lunge Peck (paired t-test, NS).

**Performance:** Lunge Peck was used equally by both males and females (paired t-test, NS) in 0.2% of interactions.

**Cave vs. burrow: contact behaviour**

Cave-dwelling little blue penguins used five contact behaviours; burrow-dwellers used only one. The burrow behaviour Lunge Peck was equivalent to the cave behaviours Breast Butt, Bill to Bill, Bill to Back, Bill Slapping and Bill-lock Twist in context and some elements of form but not posture (Fig. 9).

(1) **Cave Contact / Burrow Contact**

The single burrow contact behaviour, Lunge Peck differed in posture from the five cave contact behaviours but shared other components of form. The length of Lunge Peck (3.0 s) was not significantly different from the lengths of the five cave contact behaviours (ranged from 2.8 s to 5.0 s) (one-way ANOVA, NS). Lunge Peck was performed silently, as were all the cave contact behaviours except Bill Lock Twist (which used Growl, sometimes in conjunction with Aggressive Yell; Figures 1 & 2). There was no significant difference between Lunge Peck and the five cave contact behaviours in the proportion of interactions in which the behaviours were used (Lunge Peck 0.2%; cave contact behaviours 0.1% to 0.8%) (one-way ANOVA, NS).

**Overt Aggression**

The overt aggression category could be split into two sub-categories: (a) distance reducing behaviour (cave: Attack; burrow: Attack); and (b) contact behaviour (cave: Bite and Fight; burrow: Bite and Fight). The behaviours frequently led to serious injury, including head wounds and eye loss.

**Cave habitats**

(1) **Attack**

**Actors:** Territorial males (territorial females, non-territorial males and females).
Form: Territorial males Attacked by running toward the opponent with bill open and flippers slightly raised. Most attacks were performed silently but a small proportion (2.4% of cases) used the Aggressive Bark vocalization (Fig. 2). Attacks lasted an average of 3.7 s.

Performance: Territorial males Attacked in 0.5% of interactions. Territorial males did not use Attack equally at all interaction distances (Dmrt, $P < 0.01$). Territorial males performed Attack at 1-2 m significantly more than they performed Attack at any other distance ($P < 0.05$).

(2) Bite

Actors: Territorial males and females (non-territorial males and females).

Form: Actors simply bit the opponent, usually on the nape or throat but sometimes on the flippers. The Growl vocalization (Fig. 1) was used with Bite in 42.9% of cases. Actors bit for an average of 3.1 s before releasing the opponent. There was no significant difference between males and females in the duration of Bite (paired t-test, NS).

Performance: Birds used Bite in 1.2% of interactions. There was no significant difference between males and females in the proportion of interactions in which bite was used (paired t-test, NS).

(3) Fight

Actors: Territorial males (territorial females and non-territorial males).

Form: Opponents fought in two ways (Fig. 10). In Bite Nape Fight (88.1% of fights) the actor bit the opponent on the nape, swatting it with flipper blows to the head and sides while constantly twisting the nape flesh from side to side. In Bill Lock Fight (11.9% of fights) the opponents inter-locked bills and twisted one another's heads from side to side while swatting each other with flipper blows to the head and sides. The Growl vocalization (Fig. 1) always accompanied fights. Aggressive Yell (28.6% of fights) and Aggressive Bark (16.7% of fights) were used in conjunction with Growl during some fights (Fig. 2). Fights between territorial males lasted an average of 14.1 s.

Performance: Male territorials fought in 1.2% of interactions. Territorial females and non-territorials fought infrequently (<0.5% of interactions).

Burrow habitats

(1) Attack

Actors: Territorial males (territorial females, non-territorial males and females).

Form: Territorial males Attacked by leaping out of the burrow and running toward the opponent with bill open and flippers slightly raised. No vocalizations occurred in association with Attack. Attack lasted an
Figure 10. Fight modes used by both cave- and burrow-dwellers during offense.

average of 5.0 s.

**Performance:** Territorial males performed Attack in 4.2% of interactions. There was no significant difference in the rate at which Attack was used at the different interaction distances (two-way ANOVA, NS).

(2) **Bite**

**Actors:** Territorial males and females (Non-territorial males and females).

**Form:** Actors simply bit the opponent, usually on the nape or throat but sometimes on the flippers. The Growl vocalization (Fig. 1) was used in 20.0% of cases. Actors bit their opponents for an average of 46.0 s before releasing. There was no significant difference between sexes in the length of Bite (paired t-test, NS).

**Performance:** Bite was used in 0.3% of interactions. Their was no significant difference between the sexes in the proportion of interactions in which Bite was used (paired t-test, NS).

(3) **Fight**

**Actors:** Territorial males (Territorial females).

**Form:** Opponents fought in two ways (Fig. 10). In **Bite Nape Fight** (50.0% of fights) the actor bit the opponent on the nape, swatting it with flipper blows to the head and sides while constantly twisting the nape flesh from side to side. In **Bill Lock Fight** (50.0% of fights) opponents inter-locked bills and twisted heads from side to side while swatting each other with
flipper blows to the head and sides. The Growl vocalization always accompanied fights (Fig. 1). Aggressive Yell (50.0% of fights) and Aggressive Bark (33.0% of fights) were used in conjunction with Growl in some fights (Fig. 2). Fights lasted an average of 34.5 s.

**Performance:** Territorial males fought in 0.5% of interactions. No fights between territorial females were recorded while sampling.

**Cave vs. burrow: overt aggression**

Both cave and burrow dwelling little blue penguins used three overt aggressive behaviour patterns including two modes of fighting (Fig. 10).

1. **Attack**
   
   Only male territorials used Attack in both habitats. The behaviour was identical in form between habitats. Attack was performed silently, except for 2.4% of cases in caves where Aggressive Bark (Fig. 2) accompanied the behaviour. There was no significant difference between the behaviour patterns in length (cave 3.7 s; burrow 5.0 s) (two sample t-test, NS). However, burrow dwellers used Attack in a significantly greater proportion of interactions (cave 0.5%; burrow 4.2%) (two sample t-test, \( P = 0.05 \)). In both habitats, Attack tended to be performed more at 1-2 m than at other interaction distances (but the difference was not significant for burrow habitats).

2. **Bite**
   
   Both males and females used Bite equally in both habitats. The behaviour was identical in form between habitats. The behaviour was most commonly performed silently in both habitats but was sometimes accompanied by the Growl vocalization (cave 42.9%; burrow 20.0%) (Fig. 1). Burrow-dweller's Bites were significantly longer than cave-dweller's Bites in length (cave 3.1 s; burrow 46.0 s) (two sample t-test, \( P < 0.01 \)). There was no significant difference between the habitats in the proportion of interactions involving Bite (cave 1.2%; burrow 0.3%) (two sample t-test, NS).

3. **Fight**
   
   Only territorial males fought commonly in both cave and burrow habitats. The two fight types, Bill Lock Fight and Bite Nape Fight, were used in both habitats but not in equal proportions (cave: Bill Lock 11.9%, Bite Nape 88.1%; burrow: Bill Lock 50.0%, Bite Nape 50.0%). Fights in burrow habitats were significantly longer than fights in caves (caves 14.1 s; burrows 34.5 s) (two sample t-test, \( P < 0.05 \)). There was no significant difference between habitats in the proportion of interactions in which fight was used (cave 1.2%; burrow 0.5%) (two sample t-test, NS).

Results are summarized in Table I.
Table 1. Summary of territorial cave- and burrow-dweller agonistic repertoires. Brackets around female symbols under "Actors" mean that females performed the behaviour significantly less than males (Paired t-test or one-way ANOVA). Vocal components are listed from most common to least common. A one-way ANOVA was used to compare the length of equivalent behaviour between male and female cave- and burrow-dwellers. Distance from opponent was compared qualitatively using the results of a two-way ANOVA for behaviour in each habitat type. Variation between cave- and burrow-dwelling males and females in the proportion of interactions in which equivalent behaviour were used was tested with a one-way ANOVA.

<table>
<thead>
<tr>
<th>CLASSIFICATION</th>
<th>CAVE</th>
<th>BEHAVIOUR</th>
<th>ACTORS</th>
<th>VOCAL COMPONENT</th>
<th>COMPARISON</th>
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- **Stationary Behaviour**
  - **Defensive**
    - **Direct look**
      - d or f
    - **Point**
      - d or f
    - **Bend, Flip, Spread**
      - d or f
    - **Bur. Flip, Spread**
      - d or f
    - **Bur. Mutual Display**
      - Par: d, Gray
    - **Up, Mutual Display**
      - Par: d, Gray
  - **Offensive Behaviour**
    - **Bend, S.D.**
      - d or f
    - **Bur. Flip, Spread**
      - d or f
    - **Bur. Mutual, Adv.**
      - Pair: Gray
  - **Contact**
    - **Bill to Bill**
      - d or f
    - **Bill Slapping**
      - d or f
    - **Rear Butt**
      - d or f
    - **Bill to Back**
      - d or f
    - **Bill Lock/Quick**
      - d or f
  - **Open Aggression**
    - **Attack**
      - d or f
    - **Rate**
      - d or f
    - **Fight**
      - d or f

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<tr>
<th>COMPARISON</th>
<th>BEHAVIOUR</th>
<th>ACTORS</th>
<th>VOCAL COMPONENT</th>
<th>Length</th>
<th>Distance from Opponent</th>
<th>Proporation of Interactions</th>
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- **Significantly greater, P<0.05**
- **P<0.01**
- **P<0.001**
- **N.S., not significant**

Equivalent behaviours: See text for details.
**Egg Transfer Experiment**

There were no obvious differences between transferred and local chicks, of either habitat, in their ability to survive to the fledging stage (i.e. neither cave- or burrow-bred chicks appeared to have a competitive edge in either habitat).

Of the 22 manipulated clutches in cave habitats, ten led to the successful fledging of at least one chick. In four of the successful clutches, both the transferred and local chick survived to fledge. In three of the successful clutches, only the transferred chick survived to fledge and in the final three successful clutches, only the local chick survived to fledge.

Similarly, of the 22 manipulated clutches in burrow habitats, eleven led to the successful fledging of at least one chick. In two clutches, both the transferred and local chick survived to fledge. In four of the successful clutches, only the transferred chick survived to fledge. In the final two successful clutches, only the local chick survived to fledge.

Figure 11 shows how frequently each agonistic behaviour was used by the three classes of cave-reared chicks. The results are based on observations of approximately 400 agonistic interactions (i.e. 50 ± 15 interactions from each of three transferred chicks; 40 ± 15 interactions from each of three local chicks raised with a transfer; and 31 ± 5 interactions from each of four local chicks raised with their natural siblings).

Chicks which were bred and raised in caves used 14 different agonistic behaviours during agonistic interactions with adults or like-aged chicks. These included nine of the 17 behaviours typically used by cave-dwellers, three of the five behaviours used by both cave-and burrow-dwellers, and two of the eight behaviours typically used by burrow-dwellers (Fig. 11).

Only two of the chick behaviours listed in Figure 11 were not used by both classes of locally bred and raised chicks. Local chicks raised with a transferred chick were not observed using the burrow-dweller behaviour Lunge Hiss and local chicks raised with their natural sibling were not observed using the cave-dweller behaviour Bill to Back. This difference is probably attributable to the rarity of these behaviours with respect to sample size of chick behaviour.

Transferred chicks used all but one (i.e. Bill to Back) of the agonistic behaviours used by locally bred and raised chicks (Fig. 11). Again, this minor difference is probably due to the rarity of Bill to Back with respect to the sample size. Also, note that transferred and locally bred chicks used each agonistic behaviour at a similar frequency (Fig. 11).
Figure 11. The proportion of agonistic interactions in which behaviours were used by three classes of cave-reared young (i.e. open bars - local chicks raised with their natural siblings; hatched bars - local chicks raised with a transferred chick; and solid bars - transferred chicks raised with a local chick). The chick behaviours are organized into three categories (i.e. cave - behaviours represented in the repertoire of adult cave-dwellers; burrow - behaviours represented in the repertoire of adult burrow-dwellers; and common - behaviours represented in both cave- and burrow-dweller repertoires). Behaviours within each category are ordered with respect to how commonly they were used by local chicks raised with their natural siblings (i.e. left - most common behaviours; right - least common behaviours).
For example, both transferred and locally bred chicks used the behaviours Direct Look, Point, Indirect Look and Face Away most frequently during agonistic interactions (Fig. 11). Rare behaviours for both locally bred and transferred chicks included Directed Flipper Spread, Bill to Back, Bite and the two burrow behaviours, Lunge Hiss and Lunge Peck (Fig. 11).

These results clearly suggest that chicks were not genetically bound to the use of a habitat-specific repertoire of agonistic behaviours.

The *ad libitum* observations of chicks at manipulated nests in the burrow habitat lend further support to this conclusion. Eight agonistic interactions involving transferred chicks (*N* = 4) in the burrow habitat were observed. In five of the eight interactions, the transferred chicks used the burrow-dweller behaviour Lunge Hiss. In two interactions, transferred chicks used the burrow-dweller behaviours Bill Vibe or Directed Flipper Spread. The behaviour Face Away was used in one interaction.

Local chicks (*N* = 3), observed during *ad libitum* samples, used the burrow-dweller behaviour Lunge Hiss in two of four agonistic interactions seen. In one interaction the burrow-dweller behaviour Lunge Peck was used and in the final interaction Face Away was used. However, observation boxes were not used in the experimental burrow colony and behaviours which were typically performed from within the burrow (e.g. Strech-neck Look; Bill Vibe) were less likely to be observed.

Detailed observations of the development of different agonistic behaviours in the two habitats were not made. However, *ad libitum* observations indicated that up to approximately two or three weeks of age, chicks in both habitats developed and used only burrow-dweller behaviours. Differences between cave- and burrow-dwelling chicks became apparent as chicks became more mobile (i.e. 4 weeks of age). Gradually, cave-dwelling chicks reduced their use of burrow-dweller behaviours and replaced them with behaviours typical of cave-dwelling adults. In burrow habitats, chicks continued to use the burrow-dweller behaviours throughout development, gradually extending the number of behaviours they were capable of performing.

**DISCUSSION**

Little blue penguins had an extensive repertoire of agonistic behaviour, which varied dramatically in size and form between cave and burrow habitat types. Cave-dwelling little blue penguins used a total of 22 agonistic behaviour patterns (with 54 variations). Burrow birds used a total of 13
agonistic behaviour patterns (with 29 variations). The variations on base
behaviour patterns were mainly the result of differences in vocal
accompaniment. Cave-dwellers used twice as many defensive behaviours
(cave: 4 with 6 variations; burrow: 2 with 3 variations); twice as many
offensive behaviours (cave: 15 with 38 variations; burrow: 8 with 16
variations); and approximately the same number of overtly aggressive
behaviours (cave: 3 with 10 variations; burrow: 3 with 9 variations).

Despite variation between habitats, a number of behaviour patterns were
very similar in form (posture, length, movement, presence or absence of
vocal components) and context (distance from intruder, proportion of
interactions involving the behaviour). Both cave and burrow repertoires
had the same vocal components accompanying behaviours (with the exception
of Hiss, which only burrow-dwellers used). Also, general characteristics
of agonistic behaviour remained consistent. For example, both cave- and
burrow-dweller repertoires could be divided into three discrete
categories: defensive behaviour, offensive behaviour and overt aggression.
The defensive behaviour category for each habitat could be divided into
stationary and distance increasing behaviour. The offensive behaviour
category for each habitat could be further sub-divided into three discrete
sub-units: stationary behaviour, distance reducing behaviour and contact
behaviour. The overt aggression category for both habitats could be
divided into distance reducing and contact behaviour. In both habitats
defensive behaviours tended to be used most at low interaction distances
(i.e. < 1 m to 1-2 m). Offensive stationary behaviours, in both habitats,
were performed most commonly at mid- to higher interaction distances (i.e.
2-3 m to > 3 m). Distance reducing behaviour in both habitats tended to be
performed most commonly at middle interaction distances (i.e. 1-2 m to 2-3
m). Also, males in both habitats tended to be involved in a higher
proportion of agonistic interactions than females. In both habitats,
females were rarely involved in fights or attacks.

These results clearly demonstrated that little blue penguins did not
possess a single 'fixed' repertoire of agonistic behaviour. However,
similarities between habitats in the basic structure of repertoires, and
the overlap in the form and context of many social behaviour patterns,
suggested a common 'social predisposition' (Mason 1978). This social
predisposition may dictate 'ground rules' for agonistic behaviour in little
blue penguins but may also allow for considerable flexibility in repertoire
outcomes dependent on individual history and/or environmental circumstances
(Lott 1984). Whether such variation was adaptive or not is open to debate.
It is possible that inter-population differences were the result of random genetic or cultural changes, which did not influence individual fitness. Explanations for the occurrence of intraspecific variation in social behaviour are usually considered at two logical levels: (1) the proximate factors which may initiate alternative behavioural systems; and (2) the ultimate functional consequences that determine their maintenance or evolutionary stability (Dunbar 1982). Below I outline mechanisms which may be responsible for intraspecific variability in the little blue penguin social repertoire. I conclude with a possible explanation for why intraspecific variation in little blue penguins is maintained between cave and burrow colonies.

Possible Mechanisms for the Origin of Intraspecific Variation

Genetic phenomena

Variation in behaviour between isolated populations may reflect genetic differences in some cases (e.g. Seghers 1974). However, cave and burrow colonies of little blue penguins frequently occur side by side and there is little evidence for strong philopatry or isolation (C. N. Challies, pers. comm.). The egg transfer experiment demonstrated that chicks bred in a burrow colony, but raised in a cave, develop the same agonistic repertoire as chicks which were both bred and raised in a cave. Furthermore, both transferred and locally bred chicks used each agonistic behaviour in a similar proportion of interactions. Although this does not totally preclude the possibility of genetic variation, it suggests an overwhelming dominance or overriding effect by cultural factors.

An alternative explanation is that little blue penguins possessed two or more genetically mediated developmental programs. Developmental conversion, a form of developmental plasticity, occurs when environmental cues activate alternate developmental programs leading to specific phenotypic responses (Smith-Gill 1983; see also Schmalhausen 1949 and Lloyd 1984). A specific cue(s), distinguishing habitat type, may lead to habitat-specific social repertoires by switching between genetically established developmental programs. However, it seems unlikely that a flexible phenotypic character like behaviour would be constrained to a few developmental programs in the way that morphological characters may be, especially in species like little blue penguins, which have the potential to occupy a wide variety of habitats. The extremely variable range of habitats would be expected to favour the occurrence of 'open systems' (Mayr 1974) which allow for immediate and flexible behavioural responses to a range of circumstances (Emlen 1976).
Phenotypic modulation

A second form of developmental plasticity, phenotypic modulation, may explain intraspecific variability in little blue penguin agonistic repertoires. Phenotypic modulation occurs when phenotypes vary continuously and non-specifically in relation to environmental heterogeneity (Smith-Gill 1983; see also Schmalhausen 1949 and Lloyd 1984). Differences in the rearing environment might cause variation in little blue penguin social behaviour by altering the rates or degree of expression of a single developmental program. It is clear that variation in social environment can have a major influence on behavioural ontogeny (Bekoff & Byers 1985). These influences are critical to the kind of relationships animals have and therefore to the form of social behaviour (Bekoff 1978b; Altmann & Altmann 1979; Lott 1984). Behavioural differences occurring due to phenotypic modulation are not necessarily adaptive (Smith-Gill 1983).

Experience

Intraspecific variation in social behaviour may reflect local traditions obtained culturally through processes like habituation, sensitization, classical conditioning, instrumental conditioning, latent learning, observational learning, imprinting and other early experience effects (Lott 1984). Learning may have an especially important role in generating alternative behavioural systems in disparate circumstances (Caro & Bateson 1986). 'Behavioural discoveries' made by adults or young that influence fitness may be incorporated into social repertoires by cultural evolution (Bonner 1980). If opportunities to make discoveries and assimilate them differ between cave and burrow habitats, variation in social repertoires might be expected. The young of many vertebrates are characterized by their ability to make behavioural discoveries through exploration and interaction, and for their capacity to modify behaviour (Immelmann 1972; 1975; Mainardi 1980). In the context of little blue penguins, burrow young arc isolated from all individuals other than parents and siblings, while cave young interact with parents, siblings, neighbouring adults, non-territorial adults and non-siblings; creches of 4-6 young commonly form in caves (creches rarely form in burrow colonies). Hence, the larger and more diverse social repertoire evident in cave populations may be the result of greater opportunities to discover, learn, modify and assimilate new behaviour.

Circumstantial constraints

A final possibility is that intraspecific variability in social behaviour demonstrated here is not the result of cultural or genetic variation
between individuals, but rather, the result of the same basic phenotypes using different behaviour in different habitats (Lott 1984). Variable agonistic repertoires may simply be the consequence of physical constraints which make the performance of certain behaviour patterns impossible in some habitats. Individual phenotypes may have the capacity to perform all agonistic behaviour listed for little blue penguins in both habitats. When occupying a burrow, the burrow repertoire is used since physical constraints preclude the use of alternative behaviours or because nest sites are most economically defended using the ‘hermit crab-like’ entrance-way behaviour adopted in burrow habitats. In caves, where there are no physical barriers, a different and wider range of behaviours is possible and is employed by the same basic phenotype. *Ad libitum* observations of little blue penguins breeding under dense native vegetation in the Chatham Islands may support this hypothesis since these penguins used some elements of both cave- and burrow-dweller repertoires.

If variation was based on circumstantial constraints, a burrow bird would be capable of switching to a cave repertoire when in the cave context. As part of a study examining intraspecific variation in little blue penguin sexual repertoires (Waas, in prep.), I transferred about-to-fledge young between cave and burrow habitats. The results show that young return to the habitat from which they were released and occupy nest sites in those habitats using appropriate behaviour. These preliminary results support the hypothesis that variation is based on circumstantial constraints. However, it is possible that transferred birds acquired appropriate behaviour through learning or experience between the time of release and the return to colonies 1-2 years later.

**Why is Intraspecific Variation Maintained?**

Habitat type and resource distribution affect the development of social behaviour and may have an important influence on the evolution of social systems (Dunbar 1982; Slobodchikoff 1984; Bekoff & Byers 1985). Little blue penguins occupy a wide range of habitats. The social and physical properties of nesting areas and the distribution of two major resources, breeding sites and partners, varies greatly between habitats. In caves, resources are clumped; in burrow habitats, they are spaced linearly along coastlines. The clumped distribution of resources, and the presence of other conspecifics using dry subterranean nest sites in caves, leads logically to high interaction rates. In burrow colonies, the spaced distribution of isolated and physically enclosed nest sites leads to low interaction rates.
Plasticity of behaviour allows immediate and potentially adaptive phenotype change in response to varying environmental circumstances (Immelmann 1975; Bateson 1985). Regardless of how intraspecific variation in agonistic behaviour has come about in little blue penguins, variation in the size and form of agonistic repertoires could only be maintained if their influence on individual reproductive success was neutral or advantageous. Despite cave-dwellers having a significantly higher agonistic interaction rate, a colonial breeding formation (i.e. much higher breeding densities), and the lack of physical barriers between nest sites, there was no significant difference between habitats in the proportion of interactions involving the overt aggressive behaviours Bite and Fight, and there was a significantly lower occurrence of Attack in cave habitats. Also, cave-dwellers' fights and bites were significantly shorter in duration than those of burrow-dwellers. The diverse cave repertoire and variation in the characteristics of agonistic behaviour patterns may be the result of a flexible behavioural response that reduces the chances of any one encounter leading to or ending with overt aggression. The limited burrow repertoire may be an economical behavioural response to a breeding habitat where nest sites are enclosed and best defended using a simple series of entranceway behaviours. Flexible social responses to a range of possible habitats and the proximity of conspecifics may be required of species breeding successfully in a range of habitats and social circumstances.
Chapter II

Agonistic communication by little blue penguins: a lag sequential analysis.

Animals use aggressive displays to gain or defend resources. But what properties do displays possess which make them effective in achieving these goals? It was once common to believe that aggressive displays revealed information on what the signalling animal is likely to do next (e.g. Moynihan 1955; Cullen 1966; Smith 1977; Caryl 1982; but see Hinde 1981). This view suggested that, by displaying at one another, opponents would be able to assess which one was most willing to risk physical injury in order to secure a given resource. The most willing opponent, as indicated by the aggressive display it chose, would be expected to win.

However, the application of games theory to animal communication has identified a major problem with this view. There is no guarantee that individuals will signal correct information during aggressive interactions. An animal which always displayed a maximum intention to secure resources regardless of its actual intention would be expected to gain a definite advantage over animals which signalled honestly. If signalling in this way was heritable and increased reproductive success, populations of honest signallers would soon be overrun by cheaters. Signalling intention is, therefore, unlikely to be an evolutionarily stable strategy (ESS) (but see Maynard Smith 1979; 1982a; van Rhijn & Vodegal 1980 for some possible exceptions).

Game theorists suggest that aggressive displays may simply function to reveal properties of the signaller (e.g. body size or weapon size) which influence the animals resource holding potential (RHP) (e.g. Parker 1974; Maynard Smith 1982b). Asymmetries between opponents in RHP, as identified by displays, could be used to settle disputes since they are guaranteed to be reliable. However, this view does not help us to understand why animals use so many different aggressive displays (e.g. Tinbergen 1959; Andersson 1980). If the sole function of aggressive displays were to reveal RHP, we might expect just one or a few different displays in any given repertoire.

Furthermore, a number of studies indicate that certain displays in an animal’s repertoire are more effective than others in causing its opponents to flee (e.g. Stokes 1962a, b; Dunham 1966; Dingle 1969; Andersson 1976; but see Caryl 1979). Also, several studies have demonstrated that displays
can sometimes be used to predict the next behaviour of signalling animals (e.g. Blurton-Jones 1968; Caryl 1979; Nelson 1984; Hansen 1986; but see Paton & Caryl 1986). None of these findings are consistent with the contemporary games theory view. However, Enquist et al. (1985) have recently formulated a simple cost-benefit model which may explain these anomalies and unify games theory and traditional ethological views.

Their model demonstrates that conveying information on motivation can be an ESS provided that displays are guaranteed by a performance cost (i.e. as measured by the risk of sustaining physical injury during the performance of the displays). Thus an animal can signal a strong motivation to secure a given resource by choosing a display (e.g. one involving approach) which places both itself and the opponent in a potentially dangerous situation. By using a range of different displays, each with a different performance cost, animals could communicate information on the value of the resource for the animal. Cheaters cannot invade such a system since it is impossible to fake taking a risk.

A lag sequential analysis of agonistic interactions between cave-dwelling little blue penguins, *Eudyptula minor*, indicated support for Enquist et al.'s model of aggressive communication. The lag sequential technique, used and described in the present paper, was first developed by psychologists in the late 1970's and early 1980's (e.g. Sackett 1979; Allison & Liker 1982; but see also Dawkins & Dawkins 1976) and has yet to be fully exploited by ethologists. The technique offers several advantages over Markovian methods (see Sackett et al. 1979) and provides sequential information which is not available from simple one-step contingency measures.

Little blue penguins are highly aggressive, particularly during their nocturnal visits to colonies during the breeding season. Contests for resources (e.g. nest sites and sites used in mate attraction) are frequent and are usually settled without overt aggression. Contests which do escalate to physical combat (c. 1.2% of agonistic interactions involving males), commonly result in serious flesh wounds and eye loss. Given the serious implications of these types of injuries on foraging ability, reproductive success and survival, escalation during contests can be viewed as entailing considerable risks or costs to little blue penguins.

In the present chapter, I present evidence which suggests that little blue penguins may use the cost or risk asymmetries that exist between behaviours in their agonistic repertoire to signal motivation. The results of a lag sequential analysis indicate that: (1) little blue penguin agonistic
behaviours differ in performance cost; (2) high cost aggressive displays are more effective in deterring opponents than lower cost displays; and (3) aggressive displays can be used to predict what the signalling animal will do next. I argue that aggressive displays evoke and advertise risks being taken by actors. By using a series of displays which differ in risk, a little blue penguin can communicate to its rival its motivation to secure resources.

METHODS

Over three breeding seasons (June-February, 1984-1987) I collected approximately 150 h of focal animal observations (see Altmann 1974) from little blue penguins inhabiting two cave colonies on Banks Peninsula, New Zealand (see Chapter I for details). Records were kept during a total of 398 focal animal sessions (each 20-25 min long) with four types of focal animal: (1) territorial males \( (N=29) \); (2) territorial females \( (N=29) \); (3) non-territorial males \( (N=13) \); and (4) non-territorial females \( (N=13) \).

Territorial birds were defined as those that occupied and defended nest sites; non-territorial birds did not have nest sites, but still defended a personal space.

Observations were conducted twice weekly and were distributed evenly over the three breeding seasons. Focal animal sessions were recorded from 1 h after dusk to 0200 hours or from 2400 hours to 1 h before dawn. A standard sampling 'circuit' was established and followed starting with a different focal animal each night. Focal animals were marked with numbered metal flipper bands or were recognized by distinctive patterns on their flippers.

The sex of focal animals was determined by noting position during a minimum of three copulations, since reverse copulation has been observed in other penguin species (e.g. Richdale 1941).

All focal animal sessions were recorded with a Zeniscope Night Vision System (Model NVC-100) in conjunction with a National Panasonic video recorder (Model WV 100) and camera (Model WV P100N) or a Sony audio recorder (Model TC-D5M). A light emitting diode or low-watt torch bulb wrapped in red Cellophane and connected to a penlight battery provided ample light for recording through the nightscope. A Nakamichi microphone (Model CM300) with a shot-gun head (Model CP-4) was mounted next to the nightscope to record acoustic behaviour. The equipment was set up 4 m away from subjects, usually behind rocks or driftwood to minimize disturbance.
Analysis of Performance Cost

Subjective Estimates

In an earlier study (Chapter I), I identified and described 22 distinct agonistic displays used by cave-dwelling little blue penguins during aggressive interactions. In the present study, I use four criteria to provide a subjective ranking of the displays in order of increasing cost as measured by the risk of sustaining an injury during the performance of the displays:

1. Movement. Displays which involve moving toward the opponent are considered to have a higher cost than displays performed while stationary or displays which involve moving away from the opponent.

2. Distance. Displays initiated near or in contact with the opponent are considered to have a higher cost than displays performed at greater distances.

3. Orientation. Displays which involve orienting the head toward the opponent are considered to have a higher cost than displays with postures that shield the head and eyes.

4. Conspicuousness. Displays which have components that make the actor easy to locate (e.g. vocalizations, postures which reveal the penguins white underside) are considered to have a higher cost than displays which make the actor's presence and position less obvious.

Quantitative Estimates

I obtained quantitative estimates of how costly agonistic behaviours were to perform by determining how likely opponents were to retaliate with overt aggression (i.e. attack, bite, fight) following the performance of each agonistic behaviour used by actors (see Enquist et al. 1985; Popp 1987). Using this type of estimate, the behaviours during which actors were most likely to be attacked are considered most costly to perform. Costs associated with energy expenditure or lost time were not considered in my estimates, but these did not appear to vary much between behaviours used by little blue penguins.

Lag Sequential Analysis

Lag sequential analysis (Sackett 1979; 1980) is a technique used to identify non-random sequences of behaviours or 'events' occurring during social interaction. For 'event sequence data' (see Sackett 1979), interactions are organized as a train of events, with each event occupying a single 'unit'. An event of interest is selected as the 'criterion' (in practise, each event occurring in the sample takes its turn as the criterion). For each criterion, a count is made of the number of times
that all other recorded events occupy: (a) the very next unit (Lag 1); (b) the second unit after the criterion (Lag 2); (c) the third unit after the criterion (Lag 3) and so on to the maximum unit of interest. The same can be done for units preceding each criterion (i.e. Lag -1; Lag -2 and so on).

The observed or 'conditional' probabilities for each event at a specified lag from the criterion are calculated by dividing the number of times the event occurred at that lag by the total number of times the criterion occurred in the data. The expected or 'unconditional' probabilities for each event, calculated by dividing the total number of times the event occurred in the data (regardless of lags) by the total number of occupied units in the sample, are subtracted from the conditional probabilities. This difference is divided by an error term to produce a statistic resembling a z-score.

The z-statistic generated by lag sequential analysis approximates a standardized normal distribution. Therefore, z-scores with an absolute value greater than 1.96 indicate a statistically significant relationship (at the $P < 0.05$ level) between the occurrence of a given event (at a specified lag) and the occurrence of the criterion. A positive z-score exceeding 1.96 means that the event being considered is more likely to occur than is expected at the lag specified from the criterion. A negative value exceeding 1.96 means that the event is less likely to occur than is expected. For a more detailed discussion of lag sequential analysis and a step by step outline of the procedures employed, see Bradbury & Fincham (in press).

The ELAG program (Bakeman 1983) was used to compute lag sequential statistics for aggressive interactions of little blue penguins. I used the Allison & Liker (1982; see also Wampold & Margolin 1982) z-score computation. Aggressive interactions, transcribed from each focal animal session, were represented by a train of events alternating between the focal animal's behaviour and the opponent's behaviour (e.g. focal's behaviour / opponent's behaviour / focal's behaviour / opponent's behaviour and so on).

For each aggressive display (i.e. criterion), I examined which behaviours were most likely and which were least likely to occur at Lag 1 (the opponent behaviour following the criterion), Lag -1 (the opponent behaviour preceding the criterion), Lag 2 (the actor's behaviour following its display and the opponent's Lag 1 behaviour) and Lag -2 (the actor's behaviour preceding its display and the opponent's Lag -1 behaviour).

By comparing the behaviour at Lag -1 to the behaviour at Lag 1, I could
estimate the effect that each aggressive display had on the opponent. By examining the behaviour at Lag 2 with respect to the opponent's behaviour at Lag 1, I could estimate what if anything the different aggressive displays predicted about the actor's next behaviour. I examined the behaviour at Lag -2 to determine what caused the Lag -1 distribution and what behaviours predicted the aggressive display used as the criterion.

Only four types of aggressive interactions were analyzed: (1) territorial males defending nest sites against non-territorial intruders (from here on 'type 1' interactions); (2) territorial females defending nest sites against non-territorial intruders (from here on 'type 2' interactions); (3) non-territorial males defending calling sites (i.e. used for mate attraction) or personal space against non-territorial intruders (from here on 'type 3' interactions); and (4) non-territorial females defending personal space against non-territorial intruders (from here on 'type 4' interactions). Both the focal animal and the intruder had to be alone at the time of the interaction for it to be considered for the data set.

By imposing these restrictions, the sample of focal animals used in the analysis was reduced to 16 territorial males (c. 15 interactions from each male; range 2-28), 13 territorial females (c. 6 interactions from each female; range 2-19), 14 non-territorial males (c. 6 interactions from each male; range 1-16), and 5 non-territorial females (c. 6 interactions from each female; range 1-24). Interactions were typically 8-13 events in length.

RESULTS

Categorizing Agonistic Behaviour

Subjective Categorization

Six categories of agonistic behaviours were observed during the aggressive interactions of little blue penguins. Below I rank these categories in order of increasing cost as estimated by the four ranking criteria (i.e. movement, distance from the opponent, orientation, and conspicuousness). The 'distance increasing' (Level 1) and 'stationary defensive' (Level 2) categories included all behaviours which were estimated to reduce the risk of sustaining an injury during interactions (i.e. submissive displays). The 'stationary offensive' (Level 3), 'distance reducing' (Level 4) and 'contact' (Level 5) categories included all behaviours which were estimated to increase the risk of sustaining an injury during interactions (i.e. aggressive displays). The Level 6 category included all behaviour associated with overt aggression. The data
used to rank categories are from Chapter I. Chapter I also provides a complete description of each behaviour identified below.

(1) Distance increasing behaviour (Level 1). This category included two displays: Low Walking and Submissive Hunch. Both behaviours involved moving directly away from the opponent. The birds assumed a hunched posture with the head extended away from the opponent. Submissive Hunch was used most commonly when the opponent was within 1-2 m, while Low Walk was also used at greater distances. Neither display had a vocal component.

(2) Stationary defensive behaviour (Level 2). This category included two displays: Face Away and Indirect Look. Both behaviours involved turning the body away from the opponent while looking back toward it obliquely. However, unlike distance increasing behaviours, the actors did not move away from the opponent. The opponent was typically within 1-2 m when the displays were initiated. The displays were usually performed without vocal components.

(3) Stationary offensive behaviour (Level 3). This category included three displays: Direct Look, Directed Flipper Spread, and Point. All behaviours involved turning the body directly toward the opponent with the bill held forward. However, the actors did not move toward the opponent. Point was used most frequently when the opponent was 1-2 m away. Directed Flipper Spread was typically performed when the opponent was 2-3 m away. Direct Look was usually performed when the opponent was > 3 m away. All three displays were commonly performed with a vocal component, although less frequently during Direct Look (note: a fourth stationary offensive behaviour, Bowed Flipper Spread, was excluded from this category since the lag sequential analysis revealed that it was a 'triumph' display, used only by winners at the end of interactions).

(4) Distance reducing behaviour (Level 4). This category included two displays: Zig-zag Approach and Direct Flipper Spread Approach. During Zig-zag Approach the actor moved toward the opponent slowly. During Direct Flipper Spread Approach the movement was rapid. For both displays, the body was turned directly toward the opponent with the bill held forward. The behaviours were initiated most commonly when the opponent was 1-2 m away. Both displays were commonly performed with a vocal component.

(5) Contact behaviour (Level 5). This category included 5 displays: Bill to Back, Breast Butt, Bill to Bill, Bill Slap, and Bill Lock Twist. All five behaviours were performed while facing the opponent. Breast Butt and Bill to Back involved pushing against an opponent which was facing away from the actor. The other displays were performed while stationary and
involved contact with an opponent which was facing toward the actor. With the exception of Bill Lock Twist the behaviours were typically performed without a vocalization.

(6) Overt aggression (Level 6). This category included 3 behaviours: Attack, Bite and Fight. Attacks simply involved leaping toward the opponent with an open bill and usually occurred when the opponent was within 1-2 m. If the opponent had its back to the actor, the actor bit hold of the nape and swatted the opponent from behind with flipper blows to the head and sides (i.e. Bite Nape Fight). If the opponent was facing the actor, the actor bit the opponent's bill and twisted the opponent's head from side to side while swatting it with flipper blows to the head and sides (i.e. Bill Lock Fight). All three behaviours were commonly accompanied by vocalizations.

Quantitative Categorization

The quantitative estimates of performance cost did not provide conclusive support for the ranking obtained by using the subjective estimates (Table I). I considered only type 1 and 2 interactions in the quantitative estimates since overt aggression was extremely rare in the other types of interactions. When considering only the aggressive behaviours, it was apparent that actors were more likely to be attacked during the performance of a high risk aggressive display (i.e. level 5) than they were during the performance of a lower risk display (i.e. level 3 or 4; Table I). However, during type 1 interactions, actors were also likely to be attacked when using the low risk submissive displays (i.e. levels 1 & 2). Although this was not the case for type 2 interactions, it is apparent that the quantitative and subjective estimates of behaviour cost are inconsistent.

Table I. z-scores for the likelihood that an opponent will use overt aggression in response to the agonistic behaviour of actors*

<table>
<thead>
<tr>
<th>Type of Interaction</th>
<th>Category of Agonistic Behaviour</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>level 1</td>
</tr>
<tr>
<td>Type 1</td>
<td>+1.73</td>
</tr>
<tr>
<td>Type 2</td>
<td>+0.80</td>
</tr>
</tbody>
</table>

* Type 1, territorial males vs. non-territorial intruders; Type 2, territorial females vs. non-territorial intruders; see text for details
Risk Level Analysis

Using the subjective estimates of behaviour cost I distinguished six general categories of agonistic behaviour: two categories of submissive displays (i.e. levels 1 & 2), three categories of aggressive displays (i.e. level 3-5) and one category of behaviour associated with overt aggression (i.e. level 6). In this section I consider: (1) the effect that the three levels of aggressive displays and overt aggression had on opponents, and (2) what, if anything, the three levels of aggressive displays and overt aggression predicted about what the actor was going to do next.

Effectiveness

Figures 1 and 2 show the effect that aggressive behaviour (i.e. levels 3, 4, 5 & 6) had on opponents. Effectiveness is measured by comparing what the opponents were doing immediately prior to the actor's aggressive behaviour to what the opponent was doing immediately afterward. Below I outline the effect of each level of aggressive behaviour with respect to the four interaction types (i.e. type 1: territorial males vs. non-territorials; type 2: territorial females vs. non-territorials; type 3: non-territorial males vs. non-territorials; and type 4: non-territorial females vs. non-territorials).

(1) Level 3 behaviours (ranked as the lowest risk aggressive behaviours) were not very effective in deterring opponents (Fig. 1 & 2).

Prior to the actor using a level 3 behaviour in a type 1 or 2 interaction (Fig. 1), opponents were most likely to be using a submissive display (i.e. level 1 or 2) and were unlikely to be using aggressive behaviour (i.e. levels 3-6). Following the actor's use of a level 3 behaviour, opponents either escalated to a level 4 aggressive display (but in type 1 interactions the association with level 4 was marginal, i.e. \( z = 1.73, P = 0.08 \)) or used a level 2 submissive display.

Prior to the actors use of a level 3 behaviour in a type 3 or 4 interaction (Fig. 2), opponents were most likely to be using a submissive display (i.e. level 1 or 2) and were unlikely to be using level 3 or 4 aggressive displays. Following the actor's use of a level 3 behaviour in a type 3 interaction, the opponents were most likely to be using only a level 2 submissive display. There was no apparent relationship between the actor's use of a level 3 behaviour and the opponents response in a type 4 interaction.

(2) Level 4 behaviours (ranked as the second highest risk aggressive displays) were more effective in deterring opponents than level 3 behaviour (Fig. 1 & 2).
Figure 1. Histograms of z-scores showing the opponent’s behaviour before and after actors used each of four aggressive behaviours (i.e. from lowest to highest risk: level 3, level 4, level 5, and level 6) during the interactions of territorial males (on left) and territorial females (on right). The six categories of agonistic behaviour used by opponents are arranged from lowest to highest risk along the x-axis (solid bars are the submissive behaviours). Each bar which exceeds a z-score of +1.96 (marked by the upper dashed line) indicates an opponent behaviour which occurred significantly more often than expected ($P < 0.05$). Each bar with a z-score below -1.96 (marked by the lower dashed line) indicates an opponent behaviour which occurred significantly less often than expected ($P < 0.05$). See text for details.

Prior to the actor using a level 4 behaviour in a type 1 interaction (Fig. 1), opponents were most likely to be using either a level 2 submissive display or a level 3 aggressive display (but the association with level 3 was marginal, i.e. $z = 1.73$, $P = 0.08$) and were unlikely to be using a level 1 submissive display or a high risk aggressive behaviour (i.e. levels 4-6). Following the actor’s use of a level 4 behaviour, the opponent was most likely to be using only a submissive display (i.e. level 1 or 2) and was unlikely to be using any of the aggressive behaviours.

The effect of level 4 behaviour during type 2 interactions was similar (Fig. 1). Prior to the actor using a level 4 behaviour, opponents were
most likely to be using a level 3 behaviour and were unlikely to be using either a level 1 submissive display or a level 4 aggressive display. Following the actors use of a level 4 behaviour, the opponent was most likely to be using only a level 1 submissive display and was unlikely to be using any of the aggressive displays.

Both before and after actors used a level 4 behaviour during a type 3 interaction (Fig. 2), opponents were most likely to be using a submissive display (i.e. level 1 or 2) and were unlikely to be using aggressive displays. Therefore, Level 4 behaviour acted to keep opponents using submissive displays and stopped them from escalating as they did following level 3 behaviour. It was not possible to detect the effect that level 4 behaviour had on opponents during type 4 interactions (Fig. 2).

(3) Level 5 behaviours (ranked as the highest risk aggressive displays) were effective in deterring opponents but the influence was not as obvious as for level 4 behaviour (Fig. 1 & 2).

Prior to the actor using a level 5 behaviour in a type 1 interaction (Fig. 1), opponents were most likely to be using a level 5 behaviour, although a proportion were also likely to be using level 1 behaviours. Following the actors use of a level 5 behaviour, opponents were most likely
to be using a level 1 behaviour but the use of level 5 behaviour also continued.

The effect of level 5 behaviour was more obvious in type 2 interactions (Fig. 1). Prior to the actor using a level 5 behaviour, opponents were most likely to be using a level 5 behaviour. Following the actors use of a level 5 behaviour, opponents were likely to be using either a level 1 submissive display or a level 5 behaviour. However, the opponents use of level 6 behaviour (i.e. overt aggression) also increased to a marginally significant level (i.e. $z = 1.79$, $P = 0.07$).

Prior to the use of a level 5 behaviour in a type 3 interaction (Fig. 2), the opponents were most likely to be using a level 5 behaviour. Following the actors use of a level 5 behaviour, opponents were most likely to be using a level 1 submissive display, although the use of level 5 behaviour also continued. It was not possible to determine what behaviours were being used prior to a level 5 behaviour by the actor in a type 4 interaction (Fig. 2). However, following a level 5 behaviour by the actor, opponents were most likely to be using only a level 1 submissive display.

(4) Level 6 behaviours (ranked as the highest risk aggressive behaviours) were very effective in deterring opponents. Their effect could only be determined for type 1 and 2 interactions since overt aggression was relatively rare in type 3 and 4 interactions.

Prior to the use of a level 6 behaviour in a type 1 interaction (Fig. 1), the opponents were most likely to be using a level 2 submissive display (or perhaps a level 5 behaviour; see Fig. 1). Following the use of a level 6 behaviour by the actor, opponents were only found to use level 1 submissive displays and were unlikely to use any of the other behaviours.

Prior to the use of a level 6 behaviour in a type 2 interaction, the opponents were most likely to be using a level 5 behaviour (but the level of significance was marginal, i.e. $z = 1.79$, $P = 0.07$). Following the use of a level 6 behaviour by the actor, opponents were most likely to be using a level 1 behaviour (but again the level of significance was marginal, i.e. $z = 1.65$, $P = 0.099$).

**Predictive Value**

The predictive value of aggressive behaviours (i.e. levels 3, 4, 5 & 6) was measured by examining the relationship between a behaviour used by the actor and its very next behaviour. The measurement is made with respect to the behaviour used by the opponent. Below I outline the predictive value of each level of aggressive behaviour for each of the four interaction types.
(1) Level 3 behaviour. During type 1 interactions, level 3 behaviour predicted that the actor would escalate to level 4 behaviour \( (z = 4.34, P < 0.001) \) or continue to use level 3 behaviour \( (z = 2.77, P < 0.01) \) when the opponent responded with either a level 2 or 4 behaviour. The actor was unlikely to follow the use of a level 3 behaviour with a level 1 submissive display \( (z = -3.54, P < 0.001) \) or with a higher risk aggressive behaviour (i.e. level 5, \( z = -1.94, P = 0.052 \); level 6, \( z = -2.34, P < 0.05 \)).

Similarly during type 2 interactions, a level 3 behaviour predicted that the actor would escalate to level 4 behaviour \( (z = 3.61, P < 0.001) \) when the opponent responded with a level 2 or level 4 behaviour. Level 3 behaviour also predicted that the actor was unlikely to use a level 2 submissive display \( (z = -2.70, P < 0.01) \).

The same trend occurred for type 3 interactions. Level 3 behaviour predicted that the actor would escalate to a level 4 behaviour \( (z = 2.28, P < 0.05) \) and that it was unlikely to use a level 2 submissive behaviour \( (z = -2.88, P < 0.01) \). Again the same trend occurred for type 4 interactions but the associations were only marginally significant.

(2) Level 4 behaviours. During type 1 interactions, level 4 behaviour predicted that the actor would escalate to a level 5 \( (z = 6.93, P < 0.001) \) or level 6 \( (z = 5.63, P < 0.001) \) behaviour when the opponent responded with a level 2, 4, or 5 behaviour. Level 4 behaviour predicted that the actor would use level 3 behaviour \( (z = 4.56, P < 0.001) \) when the opponent responded with a level 1 submissive display. Level 4 behaviour also predicted that the actor was unlikely to use a submissive display (i.e. level 1: \( z = -8.11, P < 0.001 \); level 2: \( z = -2.75, P < 0.01 \)).

During type 2 interactions, level 4 behaviour predicted that the actor would escalate to a level 5 behaviour \( (z = 2.60, P < 0.01) \) when the opponent responded with a level 5 behaviour. Level 4 behaviour predicted that the actor would use a level 3 behaviour \( (z = 3.87, P < 0.001) \) when the opponent responded with a level 1 submissive display. Level 4 behaviour also predicted that the actor was unlikely to use a level 1 submissive display \( (z = -3.36, P = < 0.001) \).

A similar trend occurred for type 3 interactions. Level 4 behaviour predicted that the actor would escalate to a level 5 behaviour \( (z = 4.46, P < 0.001) \) when the opponent responded with either a level 5 or 2 behaviour. However, level 4 behaviour predicted that the actor would use a level 3 behaviour \( (z = 2.61, P < 0.01) \) when the opponent responded with a level 1 submissive display. The actor was unlikely to follow a level 4 behaviour with a level 1 submissive behaviour \( (z = -3.13, P < 0.01) \). For type 4
interactions, level 4 behaviour also predicted level 5 behaviour ($z = 2.06, P < 0.05$).

(3) Level 5 behaviour. During type 1 interactions, level 5 behaviour predicted that the actor would use either a level 3 ($z = 2.06, P < 0.05$) or a level 4 ($z = 1.98, P < 0.05$) behaviour when the opponent responded with either a level 1 or 5 behaviour, respectively. The actor was unlikely to follow the use of a level 5 behaviour with a submissive display (level 1: $z = -2.23, P < 0.05$; level 2: $z = -2.47, P < 0.05$). Level 5 behaviour could not be used to predict the behaviour of actors in type 2 interactions.

During type 3 interactions, level 5 behaviour predicted that the actor would use a level 3 behaviour ($z = 1.95, P = 0.05$) when the opponent responded with a level 1 submissive display. The actor was unlikely to follow the use of a level 5 behaviour with a level 1 submissive display ($z = -3.29, P = 0.001$). The same basic trend occurred for type 4 interactions but the associations were only marginally significant.

(4) Level 6 behaviours. During a type 1 interaction, level 6 behaviour predicted that the actor would use a level 3 behaviour ($z = 4.50, P < 0.001$) when the opponent responded with a level 1 submissive display. The actor was unlikely to follow the use of a level 6 behaviour with a submissive display (level 1: $z = -2.45, P < 0.05$; level 2: $z = -2.42, P < 0.05$). It was not possible to determine what level 6 behaviour predicted for type 2, 3, and 4 interactions.

Within Risk Level Analysis

Although the agonistic repertoire of little blue penguins could be divided into six risk levels, there was evidence to suggest that behaviour within each category also differed in terms of performance risk. For example, in the contact behaviour category (level 5) two behaviours involved contact with the opponent as it was facing away, while the other three contact behaviours involved bill to bill contact with the opponent. In terms of performance risk, the latter behaviours are likely to be more costly to perform.

Here I examine the effect and predictive value of the three stationary offensive behaviours: Direct Look, Directed Flipper Spread, and Point. Earlier I reported that Direct Look tended to be used most when the actor was > 3 m from the opponent, while Directed Flipper Spread was used most at 2-3 m and Point was used most at 1-2 m. Assuming that displays performed near the opponent entail greater risks then displays performed at greater distances, we might expect variation between the stationary behaviours in their effect on opponents and possibly in what they predict about the
actor's next behaviour.

Effectiveness

Figure 3 shows the effect that each offensive stationary behaviour had on opponents during type 1 interactions. The effect of each display is measured by comparing the opponent's behaviour before the actor's display to the opponent's behaviour after the actor's display. The results for type 2, 3 and 4 interactions were very similar or identical to those reported below.

(1) Direct Look (ranked as the lowest risk level 3 behaviour) was not very effective in deterring opponents (Fig. 3). Prior to the actor using Direct Look, the opponents were most likely to be using a level 1 submissive display and were unlikely to be using aggressive behaviours. Following the actor's use of Direct Look, opponents escalated to either a level 3 or 4 behaviour and were unlikely to be using submissive displays (i.e. levels 1 or 2).

Figure 3. Histograms of z-scores showing the opponent's behaviour before and after actors used each of three stationary offensive behaviours. On the far right are histograms showing the actor's next behaviour. See legend of Fig. 1 for details. The hatched bars (i.e. level 3a) represent the opponent's or actor's use of the behaviour being used as the criterion. Risk level 3b represents the other two stationary offensive behaviours (i.e. combined).
(2) Directed Flipper Spread (ranked as the second highest risk level 3 behaviour) was more effective in deterring opponents than Direct Look (Fig. 3). Both before and after the actor used Directed Flipper Spread, the opponents were most likely to be using a submissive display (i.e. levels 1 or 2) and unlikely to be using aggressive behaviour (Fig. 3). Therefore, it appears that Directed Flipper Spread stopped opponents from escalating to aggressive behaviour.

(3) Point (ranked as the highest risk level 3 behaviour) was also effective in deterring opponents (Fig. 3). Prior to the actor using Point, the opponents were most likely to be using a either a level 3 behaviour or submissive display (i.e. levels 1 or 2) and were unlikely to be using any other behaviour. Following the actors use of Point, opponents were most likely to be using level 1 or 2 submissive behaviours and were unlikely to be using aggressive displays.

Predictive value

Figure 3 shows the behaviour used by actors after each stationary offensive behaviour. Below I consider what each display predicted about the actor's next behaviour with respect to the opponent's response. I consider only type 1 interactions here but very similar or identical trends occurred for type 2, 3, and 4 interactions.

(1) Direct Look predicted that the actor would continue to use Direct Look if the opponent responded with a level 3 behaviour (Fig. 3). However, if the opponent responded with a level 4 behaviour, Direct Look predicted that the actor would use a submissive display (i.e. levels 1 or 2). Direct Look also predicted that the actor was unlikely to use higher risk aggressive behaviour.

(2) Directed Flipper Spread predicted that the actor would escalate to a level 4 behaviour if the opponent responded with a level 2 submissive display. However, if the opponent responded with a level 1 submissive display, Directed Flipper Spread predicted that the actor would continue to use a level 3 behaviour. Directed Flipper Spread also predicted that the actor was unlikely to use a submissive display (i.e. levels 1 or 2).

(3) Point predicted that the actor would escalate to a level 4 behaviour if the opponent responded with a level 2 submissive display (Fig. 3). However, if the opponent responded with a level 1 submissive display, Point predicted that the actor would repeat Point again. Point also predicted that the actor was unlikely to use a submissive display (i.e. levels 1 or 2).
Vocal vs. Silent Displays

Most of the aggressive displays used by little blue penguins could be performed either silently or accompanied by vocalizations (Chapter I). I suggested earlier that by using a vocal display, actors made their position and presence conspicuous to opponents and that this conferred a risk to the actor. Here I examine whether level 3 or 4 behaviours that were accompanied by vocal components differed in effect or predictive value from the same displays performed without a vocalization.

Effectiveness

Figure 4 compares the effect that silent and vocal aggressive behaviours (i.e. levels 3 and 4) had on opponents during type I interactions. The results from type 2, 3 and 4 interactions are not shown here but the findings were either very similar or the same.

1. **Silent level 3 behaviours** were not very effective in deterring opponents (Fig. 4a). Prior to the actor's use of a silent level 3 behaviour, opponents were most likely to be using submissive display (i.e. levels 1 or 2) and were unlikely to be using higher risk aggressive displays. Following the actors use of a silent level 3 behaviour, opponents either escalated to level 4 behaviour or used a level 2 submissive display and were unlikely to use a level 1, 3 or 6 behaviour.

2. **Vocal level 3 behaviours** were more effective in deterring opponents than silent level 3 behaviours (Fig. 4a). Prior to the actor's use of a vocal level 3 behaviour, opponents were most likely to be using a submissive display (i.e. levels 1 or 2) and were unlikely to be using any of the higher risk behaviours. The same was true following the actor's performance of a vocal level 3 behaviour. Therefore, it appears that vocal level 3 behaviours were effective in keeping the opponents from escalating to aggressive behaviour.

3. **Silent level 4 behaviours** were more effective in deterring opponents than either silent or vocal level 3 behaviours (Fig. 4b). Prior to the actor's use of a silent level 4 behaviour, opponents were most likely to be using either a level 2 or level 3 behaviour and were unlikely to be using higher risk behaviours (Fig. 4b). Following the actor's use of a silent level 4 behaviour, opponents were most likely to be using only submissive displays (i.e. levels 1 or 2) and were unlikely to be using any of the aggressive behaviours.

4. **Vocal level 4 behaviours** were more effective in deterring opponents than silent level 4 behaviours (Fig. 4b). Prior to the actor's use of a vocal level 4 behaviour, opponents were most likely to be using only a
Figure 4. Histograms of z-scores showing the opponent's behaviour before and after actors used vocal and silent aggressive displays: (a) vocal vs. silent stationary offensive behaviours; (b) vocal vs. silent distance reducing behaviours. On the far right are histograms showing the actor's next behaviour. See legend of Fig. 1 for details. The hatched bars (i.e. levels 3a and 4a) represent the opponent's or actor's use of the behaviours being used as criteria. Risk levels 3b and 4b represents the other level 3 or 4 behaviours (combined).
level 2 submissive display. Following the actor's use of a vocal level 4 behaviour, opponents were only likely to be using level 1 submissive display. 

**Predictive value**

Figure 4 shows the behaviour used by the actor following its use of silent or vocal behaviours (i.e. at levels 3 & 4). Below I consider what each display predicted about the actor's next behaviour with respect to the opponent's response. Only type 1 interactions are considered here but the trends described below were similar or the same for type 2, 3 and 4 interactions.

1. **Silent level 3 behaviours** predicted that the actor would escalate to a level 4 behaviour if the opponent responded with either a level 2 or 4 behaviour (Fig. 4a). A silent level 3 behaviour also predicted that the actor was unlikely to use either a vocal level 3 behaviour or a level 6 behaviour.

2. **Vocal level 3 behaviours** predicted that the actor would escalate to a level 4 behaviour if the opponent responded with either a level 2 or 4 behaviour (Fig. 4a). However, if the opponent responded with a level 1 behaviour, a vocal level 3 behaviour predicted that the actor would repeat a vocal level 3 behaviour or use a silent level 3 behaviour. A vocal level 3 behaviour also predicted that the actor was unlikely to use a submissive display (i.e. levels 1 or 2).

3. **Silent level 4 behaviours** predicted that the actor would escalate to level 6 behaviour if the opponent responded with a level 2 behaviour (Fig. 4b). However, if the opponent responded with a level 1 behaviour, a silent level 4 behaviour predicted that the actor would either use a level 3 behaviour or a level 5 behaviour (i.e. Bill to Back or Breast Butt). Silent level 4 behaviour also predicted that the actor was unlikely to use a submissive display (i.e. levels 1 or 2).

4. **Vocal level 4 behaviours** predicted that the actor would escalate to a level 5 behaviour or use a level 3 behaviour when the opponent responded with a level 1 submissive display. A vocal level 4 behaviour also predicted that the actor was unlikely to use a submissive display (i.e. levels 1 or 2).

**DISCUSSION**

Enquist et al. (1985; Enquist 1985) formulated a simple cost-benefit model of agonistic communication which showed that settling disputes on the basis of motivation can be an ESS. The model requires that there be a cost to performing agonistic behaviour (i.e. a cost measured primarily as the risk
of sustaining physical injury) and that the behaviours comprising agonistic repertoires differ in cost.

Thus, an animal's choice of behaviour can provide opponents with information on the risks that it is willing to take in order to secure the resource in question. A contestant that demonstrates, by its behaviour during a dispute, a greater willingness to take risks, is expected to win. The model, therefore, predicts a direct relationship between the cost of performing a behaviour and a behaviour's effectiveness (i.e. in deterring opponents).

In the present study I examined the aggressive interactions of little blue penguins with respect to Enquist et al.'s model (henceforth the risk-effectiveness model) and addressed three major questions: (1) Do the agonistic behaviours used by little blue penguins differ in performance risk? (2) Do agonistic behaviours differ in their effect on opponents? and (3) Can agonistic behaviours be used to predict what the actor will do next? I will discuss my findings to these questions in turn below.

Performance Risk

The risk-effectiveness model predicts that the behaviours used by animals during agonistic interactions will differ in cost as measured by the risk of injury. A comparison of cost estimates for agonistic behaviour used by little blue penguins suggested support for this prediction. I was able to divide the repertoire of cave-dwelling little blue penguins into six general categories of behaviour which could be arranged as a series of steps or levels of performance risk. Each general category was composed of two or more behaviours.

The two lowest risk categories, levels 1 and 2, contained submissive displays (i.e. behaviours which shielded the head and facilitated the ability to escape). The next three categories, levels 3, 4, and 5, contained aggressive displays (i.e. behaviours by which the actor confronted the opponent but left itself exposed to retaliation). The highest risk category, level 6, contained behaviour associated with overt aggression. The ranking criteria also indicated finer scale variation in performance risk between behaviours within each category.

Studies of aggressive communication in fulmars, *Fulmarus glacialis* (Enquist et al. 1985) and American goldfinches, *Carduelis tristis* (Popp 1987) have also provided evidence suggesting agonistic behaviours differ in performance risk (see also Andersson 1976). However, both these studies measured performance risk by calculating the proportion of times that the actor was attacked or pecked by its opponent following the performance of
each agonistic behaviour (i.e. direct cost; Enquist 1985). Thus, the behaviours ranked highest in risk were those that were followed most frequently by an attack or bite from the opponent.

When I used this technique to measure the cost of little blue penguin behaviours, I found only limited support for the ranking obtained by using the subjective estimates. Generally, when an actor used a high risk aggressive display it was more likely to be attacked than when it used a low risk aggressive display. However, when an actor used an aggressive display which was intermediate in risk, it was no more likely to be attacked than if it had used a low risk aggressive display. Furthermore, when an actor used a submissive display it was as likely or more likely to be attacked than when it used any one of the aggressive displays (see also Hayward et al. 1977; Amlaner & Stout 1978).

These anomalies suggest that there might be a problem with using 'frequency of being attacked' as the only criterion to rank agonistic behaviour with respect to performance risk. This measure could only provide a realistic estimate of performance risk if the attacks which followed each type of behaviour were equally damaging or injurious. This is unlikely to be the case.

For example, actors who are attacked during a submissive display or a low risk aggressive display are unlikely to suffer serious damage since the behaviours either shield the head or afford the actor time to protect itself against the attack. However, actors who are attacked while performing a high risk aggressive display (e.g. a behaviour which involves approaching the opponent head on) are very likely to sustain serious injury during each and every attack. Thus, one attack during a high risk display may be equivalent in overall cost to several attacks occurring during lower risk displays.

Therefore, an accurate estimate of performance cost requires measures of both how often animals are attacked when using each behaviour and how costly attacks following each behaviour are likely to be. Neither of the studies cited above or the present study have considered variation in the cost of attacks between behaviour types. Finally, none of the studies cited above, or the present study, have considered costs associated with energy expenditure or time loss during agonistic displays. Although time and energy costs associated with displaying may be significant for some species (e.g. Ryan 1988; but see Riechert 1988), these costs were unlikely to differ much between the behaviours used by little blue penguins.
Performance Risk and Effectiveness

The risk-effectiveness model predicts that high cost aggressive behaviour will be more effective in deterring opponents than low cost behaviour. In the present study I demonstrated that the behaviour of opponents was influenced by the aggressive displays of actors and that high risk aggressive displays were more effective in deterring opponents than lower risk behaviours. The magnitude of the influence appeared to depend on how costly the actor's behaviour was to perform.

Both Enquist et al. (1985) and Popp (1987) have also provided some support for this relationship (see also Paton 1986). Furthermore, other studies (e.g. Stokes 1962a, b; Dunham 1966; Andersson 1976) suggest that certain aggressive displays are more effective in deterring opponents than others. However, differences between aggressive displays in effectiveness are often slight (see e.g. Caryl 1979 and Enquist et al. 1985, Table IV). The lack of a strong relationship may be attributable to several methodological problems.

For example, the studies cited above only consider two or three types of opponent responses (e.g. did the opponent escape, stay or attack) in the assessment of a behaviour's effectiveness. By using such coarse measures, finer scale effects, such as those demonstrated in my study, are ignored. For example, an actor's aggressive behaviour might cause an opponent to use a submissive display but remain where it was. In the above studies, the actor's behaviour would not be considered effective in deterring opponents (i.e. the opponent 'stayed'). In the present study, I considered all possible opponent responses (i.e. graded in terms of performance cost) and found that, while some aggressive behaviours caused opponents to retreat, others had a lesser but still significant influence on the opponent's behaviour in the direction expected by the risk-effectiveness model (i.e. higher cost behaviours were more effective in deterring opponents than low cost behaviour).

Furthermore, the studies cited above consider only the opponent's response to the actor's behaviour when measuring effectiveness. But how can effect be measured without considering what the opponent was doing before the actor's aggressive behaviour? To measure effect we need to compare the opponent's response to an actor's behaviour with what the opponent was doing immediately prior to the actor's behaviour. Consider, for example, the following sequence of behaviour: (1) opponent approaches actor; (2) actor uses aggressive display; (3) opponent stops and looks toward the actor. In the above studies, the actor's aggressive display
would be considered ineffective (i.e. the opponent stayed). However, by considering the opponents behaviour prior to the actor's display, as I did in the present study, it becomes obvious that the display did affect the opponent's behaviour.

The relationship between the cost of aggressive behaviour and effectiveness may not be linear for little blue penguins. Effectiveness appeared to decline somewhat when both contestants escalated to the highest cost aggressive displays (i.e. contact behaviours; Fig. 1 & 2). This decline may be attributable to a high level of motivation on the part of the opponent, demonstrated by the fact that it continued interacting to the point of using contact behaviour. The greater the opponent's motivation, the less effective we might expect the actor's behaviour to be. Therefore, as contestants escalate toward the highest risk behaviours, the effect of these behaviour patterns may become less evident.

This then brings us to an important point. Do aggressive behaviours have to change an opponent's behaviour to be effective? The process of communication itself is often defined as occurring when one animal signal causes another animal's behaviour to change. However, I argue that the opponent's behaviour does not necessarily have to change after a signal for the signal to be considered effective. For example, both before and after certain aggressive displays used by little blue penguins (e.g. Directed Flipper Spread; Fig. 3), the opponents used submissive behaviour. I argue that the actors behaviour had an effect. That is, the actor's behaviour stopped its opponent from escalating to higher risk aggressive behaviours. In the present study, such behaviours were considered more effective than behaviours which were followed by the opponent escalating to higher risk behaviours.

The results of this study also show that aggressive displays accompanied by vocalizations are more effective in deterring opponents than the same displays unaccompanied by vocalizations. I argued earlier that, from the actor's perspective, behaviours with vocalizations were more costly than those without vocalizations since the actor is made conspicuous and easy to locate. However, it is not clear why the presence of a vocal component should influence the opponent. One possibility is that vocal behaviours reveal RHP.

However, an analysis of little blue penguin vocalizations (Waas, unpublished data) suggested that this was unlikely to be so. Seven characteristics of the Bray vocalization (i.e. inhalation phrase length, exhalation phrase length, elements per second during the inhalation phrase,
inhalation frequency and the three main frequencies of the exhalation phase) and three characteristics of the Growl vocalization (i.e. phrase length, elements per second for each phrase and main frequency) were measured from the calls of nineteen territorial males (> 5 calls from each) for which age and mean weight were known. Only one character of the Bray vocalization (i.e. inhalation frequency) was significantly correlated with male weight. None of the characters of the Bray vocalization was correlated with age. Also, none of the characters measured for the Growl vocalization (i.e. the most commonly used vocalization; Chapter I) was correlated with either weight or age.

A second explanation for the greater effectiveness of displays with vocal components is that vocalizations allow opponents to recognize actors which have beaten them previously (e.g. van Rhijn 1980; Bossema & Burgler 1980; van Rhijn & Vodegel 1980; Piersma & Veen 1988). However, I purposely eliminated interactions between neighbours in the present analysis to avoid this source of error (little blue penguins were unlikely to recognize non-territorial intruders since these animals were transient).

A final explanation for the greater effect of displays accompanied by vocalizations is that vocal behaviour 'highlights' the risks being taken by actors. Given that most aggressive interactions between little blue penguins occur under extremely low light conditions, opponents may have only limited visual information on what the actor is doing. By using a vocalization in conjunction with aggressive behaviour, an actor may advertise the risks that it is taking. Obviously, an opponent can only react to the actor taking risks if it is made aware that they are occurring. Thus, the greater effect of behaviours with vocal components can be explained by the possibility that risks being taken by the actor are more obvious to the opponent. A similar reasoning could be applied to other components of aggressive displays (e.g. postures) which make behaviours obvious.

**Performance Risk and Predictive Value**

The risk-effectiveness model predicts that the effect of an actor's aggressive behaviour (i.e. on the opponents behaviour) is attributable to performance cost, not to what the behaviour predicts about what the actor will do next (i.e. as has been proposed in the traditional ethological view). Furthermore, as outlined in the Introduction, signalling information on intention is unlikely to be an ESS. Therefore, we would predict that the aggressive behaviours used by little blue penguins would not be useful for making predictions about what actors are likely to do next.
The results of the present study do not support this prediction. The aggressive behaviours used by little blue penguins could be used to predict the next behaviour of actors. However, the behaviour predicted was conditional upon the opponents response to the actor's first behaviour. Generally, aggressive behaviours predicted that the actor would escalate to the next highest risk behaviour when opponents did not retreat, but predicted that the actor would reuse the same behaviour or change to a lower risk aggressive behaviour when the opponent did retreat.

Contests tended to start with aggressive displays which were low in risk (i.e. level 3) and escalate to a behaviour from the next highest risk category (i.e. level 4) when the opponent did not retreat. However, if the opponent did not retreat following a level 4 behaviour, the actor either escalated to a behaviour from the next highest risk category (i.e. level 5) or attacked the opponent (i.e. level 6). Actors did not escalate to overt aggression from a level 5 behaviour. Only level 4 behaviour predicted overt aggression. Level 5 behaviour (i.e. contact behaviour) predicted that the actor would 'step down' to lower risk aggressive behaviour (i.e. level 3 or 4) whether the opponent retaliated with a contact behaviour or retreated. The escalation process appeared to stop at contact behaviour.

One explanation for this effect is that contact behaviours allowed the opponents the opportunity to assess RHP. This seems very likely since the displays involve pushing against one another, inter-locking and twisting bills or extending their touching bills upward with bodies held upright (see Chapter I). Since RHP could be used to settle the dispute without escalating to overt aggression, the lack of continued escalation after a level 5 behaviour can be explained. The effect might also explain the ambiguous results obtained for contact behaviour when considering the effectiveness of aggressive displays. It is not, however, clear why some actors avoid using level 5 behaviour and attack instead.

The aggressive displays used by little blue penguins could also be used to predict what the actor was unlikely to do next. For example, the lowest risk aggressive displays (i.e. level 3) predicted that the actor was unlikely to follow the display with the lowest risk submissive display (i.e. level 1) or with very high risk displays such as contact behaviours or overt aggression (i.e. levels 5 & 6). However, the next higher risk displays (i.e. level 4) only predicted that the actor was unlikely to use submissive displays (i.e. levels 1 & 2). Similarly, the highest risk aggressive displays predicted that the actor was unlikely to follow with any one of the submissive displays. It is clear from these results that it
may be important to consider not only what displays predict but also what behaviours are unlikely to occur following aggressive displays.

Do these results mean that the traditional ethological view (i.e. that aggressive displays signal intention) is supported? I do not believe so. The predictability of behaviour following aggressive displays may simply be the result of an escalation process. Why should we expect actors or their opponents to demonstrate (i.e. by their choice of behaviour) the highest risk they are willing to take at the onset of the encounter? Actors should start off with low risk behaviour and escalate step by step to higher risk behaviours. By doing this the actor will always deter the opponent with the lowest risk (and therefore least costly) behaviour possible. If the lower risk behaviour suffices in deterring the opponent then the actor has not placed itself into an unnecessarily high risk situation. If the opponent is not deterred the actor simply steps up to the next higher behaviour until the opponent retreats.

A number of other studies (e.g. Stokes 1962a, b; Dunham 1966; Andersson 1976) have provided evidence suggesting that aggressive displays can be used to predict the next behaviour of signalling animals. However, as with studies considering the effect of aggressive displays, the relationship between the aggressive display used and what it predicts is often weak (see Caryl 1979; Paton & Caryl 1986). Once again, the lack of a clear relationship may be attributable to methodological problems.

For example, the studies cited above consider only two or three types of behaviour when assessing what displays predict about the signallers next behaviour (e.g. did the display predict attack, stay or escape). A step by step escalation process, like that demonstrated in the present study, would not be detectable when using such coarse measures.

Furthermore, the above studies did not consider the opponent's response to displays when attempting to determine what displays predict. This would lead to ambiguous results (Hazlett & Bossert 1965; Stout 1975; Bossema & Burgler 1980; Hinde 1981; Paton 1986; but see Nelson 1984). For example, the approach displays used by little blue penguins (i.e. level 4) only predicted attack if the opponent did not retreat. When the opponent did retreat, level 4 behaviour predicted that the actor would step down to a lower risk aggressive display. However, if the opponent's behaviour was not considered in the analysis, the relationship between the performance of a level 4 behaviour and attack would be diluted by the relationship between an opponent's retreat and the actor's consequent use of lower risk displays (see also Piersma & Veen 1988).
Conclusions

Cave-dwelling little blue penguins use a large repertoire of agonistic behaviours which appear to differ in cost (i.e. as measured by the risk of sustaining injury during behaviour performance). Disputes over resources may be settled, at least partially, on the basis of motivation (i.e. as revealed by the contestants' choice of behaviour). Contests tend to begin with low cost behaviour and escalate toward higher cost behaviour. Behaviour cost appears to be directly related to how effective behaviours are in deterring opponents, although effectiveness diminishes when both opponents escalate to the highest risk displays (i.e. when both contestants are highly motivated). Displays which make the risks being taken by the actor obvious (e.g. behaviour with vocal components) are more effective in deterring opponents than displays which do not advertise the risks being taken. Aggressive displays tend to predict that the actor will escalate to higher risk behaviour when opponents do not retreat. However, the predictive value of displays is probably the result of a simple escalation process which ensures that the opponents are deterred by the lowest risk behaviour.
Chapter III

Acoustic displays facilitate courtship in little blue penguins, *Eudyptula minor*

Social facilitation is the process by which the behaviour of one individual alters the rate at which a conspecific performs that specific behaviour (e.g. mating call) or a similar type of behaviour (e.g. courtship; reviewed in Clayton 1978). Although the term applies to any change in the performance rate of a given behaviour (e.g. Allee et al. 1950), it is primarily used to describe the incremental effects. Zajonc (1965) distinguished between the facilitating influences of presence (audience effect) and activity (coaction effect). He suggested that the 'audience effect' occurs when the 'mere presence' of a conspecific facilitates a response from perceivers. A 'coaction effect', by contrast, occurs when the behaviour of a conspecific facilitates a response from the perceivers.

In the present study I isolated coaction effects from audience effects in the little blue penguin, *Eudyptula minor*, by using playback. Surprisingly, few studies have examined the effect of coaction on courtship behaviour quantitatively (but see Fetterolf & Dunham 1985). My main objective was to determine whether vocal courtship behaviour facilitates courtship responses in little blue penguins and whether facilitation might exaggerate levels of social stimulation in their breeding groups.

The little blue penguin was used to investigate coaction effects of acoustic behaviour because its courtship behaviours have loud, obvious acoustic components. The influences of visual behaviour are limited by its nocturnal habits on land and by the visually disruptive habitats it occupies (e.g. rocky shores, caves, forests). The little blue penguin breeds in caves, burrows and under dense vegetation; nest sites are typically 2-3 m apart. The specific goals of this study were to determine whether (1) the acoustic components of courtship displays could facilitate increased levels of reproductive behaviour; and (2) the characteristics of coaction effects differed between behaviour patterns associated with courtship.
Experiments were conducted on four New Zealand colonies of little blue penguins, three on Banks Peninsula and one on Rangatira, an island in the Chathams group, during the pre-egg courtship period (July - September) of 1986. Two mutually exclusive experimental sites were chosen within each of the four colonies, and a central point in each site was selected for playback and observations. All experiments were carried out on calm evenings between 1900 and 2400 hours under low ambient light conditions. Recordings for playback were made with a Marantz PMD201 cassette recorder and a Nakamichi CM300 microphone from areas outside but near (less than 0.5 km) experimental sites. A Realistic Minimus speaker was used with the cassette recorder for playback.

Each 2 h experiment (N=47) was made up of four half-hour tests. Each test began with a 10-min control period, followed by a 5-min playback period and ended with a 15-min post-playback period. The playback consisted of single 15-20 s vocal segments separated by 30 s silent periods. Treatments included: (1) the male solo call, which is performed by unmated males outside of nesting areas and attracts unmated conspecifics; (2) the territorial mutual display, which is performed by mated pairs at their nest sites in response to territorial intrusions or after fights; (3) the sexual mutual display, which is performed by mated birds at nest sites and precedes copulations; and (4) a composite of crested penguin (Eudyptes pachyrhynchos and E. robustus) equivalents to the above displays in the same format. Eudyptes overlap Eudyptula's range and may be closely related (Zusi 1975; Stephan 1980; Jouventin 1982).

The sequence of playback treatment was selected randomly prior to each experiment. Each of the four treatments (N=47) was used once in each experiment. The amplitude of playback was matched (by ear) to a level equivalent to that 1 m from a displaying bird. Displays were typical and of approximately the same length. All three little blue penguin displays are composed of the same basic pattern: inhalation/exhalation braying (see Figure 1 in Chapter 1). Territorial mutual displays tend to have a faster delivery and higher pitch than sexual mutual displays. Sexual mutual displays can also be distinguished from territorial mutual displays by a drumming sound produced by the male patting the female's back and sides with his flippers (females evert their cloacas as the males tread on their backs and drum their sides).
Acoustic behaviour distinguished during each test was recorded onto standardized entry sheets at intervals of 1 min. The post-control period (i.e. the playback and post-playback periods) for each of the four treatments was divided into four 5-min segments and mean display rates (per min) were calculated for each. Mean display rates (per min) for the 10-min control periods were subtracted from the means of each of the four 5-min segments to obtain dependent variables (Playback, PP₁, PP₂ and PP₃) for treatments in each sampling area. Dependent variables, therefore, represent variation from calling rates before the experiment. A one-way analysis of variance was used across treatments with dependent variables of each segment represented by eight experimental sites. Orthogonal comparisons (Sokal & Rohlf 1981) were used to distinguish variation in response between: (1) the crested penguin treatment and little blue penguin treatments; and (2) the behaviour used as the treatment and the other two little blue penguin displays.

RESULTS

Two types of coaction effects facilitated increases in the rate of courtship behaviour. The first was a general significant increase in all recorded courtship responses. The second was a significantly greater facilitation of the specific behaviour used in playback (Table I; Fig. I). Responses were greatest during playback and usually dropped to control levels within 20 min (Fig. I).

Solo Calls

The solo call response to little blue penguin treatments was significantly greater than to the crested penguin treatment during Playback and the first 5 min of the post-playback period (Table I). The solo call treatment facilitated solo call responses to significantly higher levels than did either mutual display treatment during Playback, and the first 10 min of the post-playback period (Table I). There was no significant difference between the mutual display treatments on facilitation of solo calls. The solo call treatment maintained solo call response levels significantly above the levels of the crested penguin treatment throughout the Playback and post-playback periods ($P < 0.05$, Bonferroni confidence intervals; Fig. I).

Mutual Displays

The mutual display response to little blue penguin treatments was significantly greater than to the crested penguin treatment during Playback.
Table 1. ANOVA across responses to treatments (i.e. solo call, territorial mutual display, sexual mutual display and crested penguin call) for each 5-min time segment, and Orthogonal comparisons.

<table>
<thead>
<tr>
<th>Response</th>
<th>Time (5-min intervals, 1=playback)</th>
<th>ANOVA</th>
<th>Orthogonal comparison†</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>$F$</td>
<td>$P$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>($df=3,28$)</td>
<td></td>
</tr>
<tr>
<td>Solo call</td>
<td>1</td>
<td>23.373</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>7.164</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>3.408</td>
<td>0.031</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>1.499</td>
<td>0.235</td>
</tr>
<tr>
<td>Mutual display</td>
<td>1</td>
<td>12.843</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>2.923</td>
<td>0.051</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>1.193</td>
<td>0.329</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>0.455</td>
<td>0.715</td>
</tr>
<tr>
<td>Copulation</td>
<td>1</td>
<td>1.394</td>
<td>0.264</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>3.025</td>
<td>0.045</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>1.667</td>
<td>0.195</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>0.301</td>
<td>0.824</td>
</tr>
</tbody>
</table>

* See text for details
† Orthogonal comparison A: response to crested penguin treatment versus response from little blue penguin treatments. Orthogonal comparison B: response from little blue penguin behaviour used as treatment versus response from other little blue penguin treatments.

and the first 5 min of the post-playback period (Table I). Little blue penguin mutual display treatments facilitated mutual display responses to significantly higher levels than did solo call treatments during Playback (Table I). There was no significant difference between the two mutual display treatments on mutual display facilitation. Solo call treatments facilitated an mutual display response significantly different from the crested penguin treatments only in the first 5 min of the post-playback period ($P < 0.05$, Bonferroni confidence intervals; Fig. I).

Copulation

Copulation rates were significantly greater in response to little blue penguin treatments than to the crested penguin treatments during the second 5 min of the post-playback period (Table I). The sexual mutual display treatment facilitated copulation significantly more than the territorial mutual display and solo call during the first 5 min of the post-playback period (Table I). The sexual mutual display treatment maintained copulation rates significantly above the response rates to the crested
Figure 1. Mean response rates (per min) for playback treatments. The dashed line represents pre-experiment performance rates. Each histogram shows change in response rate from the initiation of playback (0 min) to the end of the post-playback period (20 min). Response change within histograms was not tested statistically. Vertical comparisons made with respect to time (i.e. follow equivalently hatched bars downward) indicate variation in response rate between playbacks, and were tested statistically. Bars with any overlapping letters are not significantly different from each other. Bars not sharing any letter are significantly different ($P < 0.05$; Bonferroni confidence limits). SC: solo call; MD: mutual display; SMD: sexual mutual display; TMD: territorial mutual display; COP: copulation; CON: composite of crested penguin calls.

penguin treatment during Playback and the first 10 min of the post-playback period ($P < 0.05$). The solo call treatment increased copulation rates significantly above the crested penguin treatment during the second 5 min of the post-playback period ($P < 0.05$, Bonferroni confidence intervals; Fig. 1).
DISCUSSION

These results are consistent with the observation that reproductive behaviour is contagious in groups (e.g. Darling 1938; Hailman 1964; Burger 1979; Coulson & Dixon 1979). Two overlapping coaction effects occurred: (1) the playback of each little blue penguin courtship display resulted in a significant increase in the rate at which courtship behaviours were performed by perceivers; and (2) the courtship display facilitated most during each little blue penguin treatment was that incorporating the acoustic components being played back. For example, the solo call treatment resulted in a significant increase in all courtship behaviours, but it elevated solo call responses to significantly higher levels than it elevated mutual displays. Furthermore, copulation, evidenced by mounting 'drums', was facilitated by the acoustic components of courtship displays.

Three studies have attempted to provide evidence for coaction effects on courtship behaviour: Fetterolf & Dunham (1985) and Southern (1974) for ring-billed gulls Larus delawarensis; and Gochfeld (1980) for the least tern Sterna albifrons. Gochfeld (1980) and Southern (1974) compared the behaviour of neighbours of copulating or displaying pairs to the behaviour of the same pairs when they were not involved in courtship. Their results demonstrated clustered courtship behaviour within groups, but not that courting birds facilitated the responses. The existence of some common influence affecting individuals simultaneously (e.g. the approach of a receptive female, intruder, or predator) could have the same effect.

Fetterolf & Dunham (1985) demonstrated that sex specific courtship calls of ring-billed gulls facilitated sex-specific courtship responses. Playback of 'combined' calls facilitated courtship behaviour and increased copulation rates significantly. However, playback of least tern copulation calls also facilitated courtship responses making interpretation difficult. In my study, playback of crested penguin calls had no effect on little blue penguin vocal behaviour or copulation rates. Sexual mutual displays, the little blue penguin equivalent to combined calls of ring-billed gulls, facilitated the greatest copulatory response in little blue penguins, but other displays facilitated copulation as well.

A number of causal hypotheses for the facilitation of behaviour have been proposed (e.g. Tolman 1968; Pallaud 1971; see Clayton 1978 for a review). The facilitation of social behaviour is most commonly interpreted at a functional level. For example, Fetterolf & Dunham (1985) suggested that facilitation of courtship in ring-billed gulls was selected to reduce the
risk of interruption and extra-pair copulation (see also Emlen 1984). Farr (1976) argued that the facilitation of male display behaviour in guppies, *Poecilia reticulata*, was the result of intra-sexual competition for mates (see also Colgan et al. 1979). Regardless of what mechanism(s) facilitates social behaviour in little blue penguins, coaction effects may influence perceivers by (1) exaggerating the number of courtship displays an individual perceives over a given period of time; (2) causing individuals to accelerate display performance over a given period of time, possibly leading to more frequent pair displays; and (3) causing pairs of individuals to copulate synchronously with local conspecifics.

Social facilitation could affect the timing and synchrony of breeding through the above effects if coaction influences the amount and distribution of social stimulation in groups (Waas, unpublished data). Seabirds breeding in groups reproduce earlier and with greater synchrony than solitary breeders (reviewed in Gochfeld 1980; but see Burger 1979 and Rodgers 1987). Social stimulation provided by the presence and courtship behaviour of conspecifics influences follicle maturation in birds (e.g. Warren & Hinde 1961; Erickson & Lehrman 1964; Brockway 1965; Lott et al. 1967; Lehrman & Friedman 1969; Erickson 1970). Providing social stimulation has a cumulative, 'tonic' effect on gonadal development (Schleidt 1973; see also Teyssedre & Halliday 1986), social facilitation might reduce the time required to attain reproductive condition by exposing individuals to greater extra-pair social stimuli (i.e. (1) above) and/or by leading individuals to court more frequently themselves (i.e. (2) above). Once reproductive condition was obtained, the facilitation of copulation (i.e. (3) above) might lead to the spatial and temporal clustering of fertilization.
The little blue penguin was used to examine three specific issues in animal communication.

In Chapter I, I examined intraspecific variation in the agonistic repertoires of little blue penguins associated with environmental heterogeneity. Although intraspecific variation in mating systems (e.g. Lott 1984) and life history (e.g. Dobson & Murie 1987) has received a considerable amount of attention, intraspecific variation in social repertoires has been largely unrecognized or ignored. This has fostered the view that social repertoires are relatively invariable and has led many ethologists, including those studying penguins (e.g. Jouventin 1982; Warham 1975), to use social repertoires as characters for interspecific comparisons of relatedness.

However, my study of agonistic repertoires used by little blue penguins in two types of breeding colonies suggested that such comparisons should be made with caution. Cave-dwellers, which nested in tight, colonial aggregations and had no physical barriers between nest sites, had large and complex agonistic repertoires. In contrast, burrow-dwellers, which nested in loose aggregations and were physically isolated from one another, had relatively small and simple repertoires. A large number of behaviours were found to be habitat specific.

Despite variation between cave- and burrow-dweller repertoires, many agonistic behaviours were similar in form (e.g. posture, duration, presence or absence of vocalizations) and context (e.g. distance from intruder when behaviours were used). Furthermore, repertoires from both habitats could be subdivided into several discrete categories (i.e. two categories of defensive behaviour; three categories of offensive behaviour; and two categories of overtly aggressive behaviour). Also, males in both habitats were involved in more aggressive interactions than females. These similarities suggested that little blue penguins may have a common social predisposition, on which all repertoires are based. However, the ultimate form and size of repertoires appears to be mediated by the social and physical properties of occupied habitats.

Also, despite cave-dwellers having significantly higher agonistic interaction rates than burrow-dwellers, cave birds attacked one another less often and used overtly aggressive behaviours with shorter durations than did burrow-dwellers. This suggested that variation in agonistic repertoires may represent a socially mediated, adaptive response to environmental conditions. Large repertoires may reduce the proportion of encounters leading to overt aggression where interaction rates are high.
In Chapter II, I examined the characteristics of aggressive interactions occurring between cave-dwelling little blue penguins. Game theory models of aggressive communication have suggested that animals are unlikely to use aggressive displays to signal motivation. However, this prediction is based on the argument that signalling intentions is unlikely to be an evolutionarily stable strategy. I argue that animals can signal motivation, but that displays indicate motivation by demonstrating a willingness to take risks (e.g. Enquist 1985), not by conveying information on intentions.

I presented evidence which suggested that the agonistic displays of little blue penguins differ in how costly they are to perform (i.e. as measured by risk of being injured during the performance of the display). Using lag sequential analysis (Sackett 1979), I demonstrated that high cost displays were more effective in deterring opponents than were lower cost displays. Furthermore, displays accompanied by vocalizations were more effective in deterring opponents than the same displays performed silently.

I also argue that aggressive displays act to evoke and advertise risks being taken by the signalling animal. An actor can signal a strong motivation to secure a disputed resource by choosing a display that places both the opponent and itself into a potentially dangerous situation. A weaker motivation is demonstrated by the use of a less costly display. A communication system based on cost is guaranteed to be reliable since it is impossible for signalling animals to fake taking a risk.

Furthermore, the results of my study demonstrated that the actor's behaviour following aggressive displays was predictable. However, this was unlikely to be the result of actors signalling intention. Rather, it appears to be the simple result of an escalation process. Actors tended to start encounters with low cost displays, and escalate step by step to higher risk behaviours when opponents were not deterred. By doing this, the actor ensures that it will always deter the opponent with the lowest risk (and therefore least costly) behaviour possible. If a low risk behaviour suffices in deterring the opponent, then the actor has not placed itself into an unnecessarily high risk situation.

In Chapter III, I examined the facilitation of courtship behaviour by acoustic displays in little blue penguins. The social facilitation of courtship behaviour, which has rarely been demonstrated, is thought to be related to breeding synchrony in groups (Gochfeld 1980). Playback of the acoustic components of each of three little blue penguin displays resulted in significant increases in the rate at which perceiving conspecifics copulated and performed courtship displays; playback of crested penguin calls as controls had no effect on little blue penguin behaviour.
Although the performance rates of courtship behaviour observed (i.e. mutual displays, copulation and male solo calls) were elevated significantly by the playback of each little blue penguin display, the courtship behaviour facilitated most was that incorporating the acoustic components being played back. I found that responses were greatest during the 5-min playback period of each test and usually dropped to control levels within 20 min. I argue that social facilitation may alter the availability of social stimuli and cluster acts of copulation, both of which may influence the timing and synchrony of breeding in groups.
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