Aggressiveness in king penguins in relation to reproductive status and territory location

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King penguins, *Aptenodytes patagonicus*, vigorously defend small territories in very dense colonies. The egg-laying season lasts approximately 4 months, but only pairs that reproduce during the first half of the period succeed in fledging a chick. I examined various factors affecting aggressiveness of king penguins during the breeding season and focused on the differences between central and peripheral territories. Pairs on peripheral territories experienced twice as many encounters with avian predators as did central birds. The vast majority of peripheral birds were late breeders, indicating that reproductive success was very low among penguins defending a territory on the edge of the colony. Time invested in territory defence and rate of agonistic encounters between breeding neighbours increased from the incubation to the brooding period. Parents gave most threat displays to territorial neighbours when the chick was very young and just before crèche formation. Distance to colony edge was not related to aggressiveness in incubating birds, however, the rate of pecking and flipper blows increased from the edge to the centre during brooding. In addition, aggressiveness of breeding penguins towards travelling birds trespassing into their territory increased with distance to edge. Early breeders were not more aggressive than late breeders but the proportion of time spent in territory defence increased with the number of days a bird had spent incubating. As expected, I did not detect any sex difference in aggressive behaviour. Birds occupying territories on the beach were generally more aggressive during the incubation period than those located on the valley sides. Reproductive status (incubating versus brooding) and territory location were the main factors explaining the various levels of aggressiveness observed in breeding king penguins.

The vast majority of seabirds nest in dense colonies where pairs vigorously defend a small breeding territory (Wittenberger & Hunt 1985). It has been proposed that productivity of seabirds may vary with location of the territory (Coulson 1968; Kharitonov & Siegel-Causey 1988). In several studies, birds occupying central territories have a higher reproductive success than peripheral birds, mainly because of a reduced risk of predation and flooding in the centre of the colony (Patterson 1965; Coulson 1968; Penney 1968; Tenaza 1971; Deixheimer & Southern 1974; Spurr 1975; Hutson 1977; Montevecchi 1978; Burger & Lesser 1979; Gochfeld 1980; Wiklund 1982; Ainley et al. 1983; Burger & Gochfeld 1990). However, some authors have reported no difference in reproductive success according to nest or territory location (Ryder & Ryder 1981; Giese 1996; Barbosa et al. 1997). In general, more predation attempts occur on the colony edge than in the centre (Taylor 1962; Penney 1968; Siegel-Causey & Hunt 1981; Emslie et al. 1995). In this situation, competition for territories is expected to be high and it is often assumed that birds nesting in the centre of a colony are more aggressive than peripheral birds in order to access high-quality central territories (Tenaza 1971; Pulliam 1973; Spurr 1974a; Hutson 1977; Kharitonov & Siegel-Causey 1988; Viñuela et al. 1995). Adélie penguins, *Pygoscelis adeliae*, that were aggressive towards an artificial penguin model, for example, occupied central territories and had a higher breeding success than less aggressive individuals (Spurr 1974a). Evidence for aggressive central territory holders, however, is rare and rather unconvincing, in part because it relies on the use of artificial bird models presented to territorial breeders (Spurr 1974a; Hutson 1977; Viñuela et al. 1995).

Other factors may influence aggressiveness in breeding birds. Parental investment theory predicts that nest defence should increase with the advent of the breeding season because the fitness value of a chick is higher than that of an egg (Williams 1966; Trivers 1972; review in...
Montgomerie & Weatherhead 1988). As offspring age, renesting potential declines, the cost of replacing the brood increases and the difference between survival probabilities of parents and young is reduced, thus increasing the future fitness benefits of the parents (Barash 1975; Andersson et al. 1980; Burger 1980; Montgomerie & Weatherhead 1988). According to these arguments, the value of a chick and the willingness of the parents to defend it should increase as chicks approach fledging. However, some authors have found that aggression is higher at hatching, when chicks are more vulnerable (Burger 1981, 1983; Burger & Gochfeld 1990). Also, extrinsic factors such as habitat type may affect the level of aggressiveness observed (Kharitonov & Siegel-Causey 1988; Burger & Gochfeld 1992).

In king penguins, Aptenodytes patagonicus, the egg-laying season starts in mid-November and lasts about 4 months, 2–3 months longer than in the majority of other penguin species (Weimerskirch et al. 1992; Jouventin & Maugé 1996). Only those adults that breed in the first half of the breeding season, however, can fledge a chick (Weimerskirch et al. 1992; van Heezik et al. 1994; Olsson 1996; Brodin et al. 1998). Survival of chicks hatched after February is very low because they do not have time to attain the critical body mass (10–12 kg) necessary to survive the subantarctic winter (Cherel & Le Maho 1985; Weimerskirch et al. 1992; van Heezik et al. 1994). Chicks are fed infrequently in winter or may not be fed at all for as long as 5 months (Cherel & Le Maho 1985; Weimerskirch et al. 1992). Consequently, the fitness value of chicks and the willingness of parents to defend them should be higher for chicks hatched by early breeders than for chicks hatched by late breeders.

King penguin pairs vigorously defend a territory of approximately 0.5 m² against breeding neighbours and intruders that approach within pecking distance (Barrat 1976; Le Maho et al. 1993). The pair incubates a single egg directly on their feet and fasts both when incubating and brooding a chick (Stonehouse 1960; Barrat 1976). Parents alternate nest duties every 5–22 days (Barrat 1976; Weimerskirch et al. 1992). Because both sexes actively defend the territory during incubation and brooding and are of very similar body size (Barrat 1976), I did not expect to find any difference in aggressiveness between males and females.

I was interested in determining what factors affect aggressiveness in breeding king penguins. Particularly, I tested the hypotheses that reproductive success is higher for central territories than peripheral territories and that individuals occupying central locations are more aggressive than birds on the edges of the colony. Also, I assessed whether breeding date, time spent incubating, sex and habitat type affected aggressiveness. Finally, I tested whether aggressiveness increases with offspring age (from egg to fledgling), as predicted by the parental investment theory.

**METHODS**

This study was conducted in the breeding colony of la Baie du Marin (40 000 pairs) on Possession Island, Crozet Archipelago (46°25’S, 51°45’E; Weimerskirch et al. 1992). Breeding birds were associated in one single colony covering approximately 25 000 m². I located pairs on their breeding territory before laying, and sprayed them at 1–2 m with a dye. The day after laying, a plastic Darwick tag was attached around the flipper of the incubating bird and the egg was marked with a permanent marker. Because the male performs the first incubation shift in king penguins (Stonehouse 1960; Barrat 1976; Weimerskirch et al. 1992), the male was marked first. The female was marked during her first incubation shift (i.e. 2–3 weeks after laying). As part of another study, some marked birds (42%) were later untagged and a number was painted on their chest with Nyanzol-D branding dye (Giese 1996). Interventions in the colony were minimized to reduce disturbance to the birds.

I knew the exact day of laying for each marked female, and pairs were observed daily during the entire incubation period to time all incubation shifts. In king penguins, hatching occurs on average 53 days after the initiation of incubation (Weimerskirch et al. 1992). Early breeders lay their egg in late November–early December (see Weimerskirch et al. 1992). Those that laid after the first hatching was observed, or those that were still incubating an egg after February, were considered late breeders (van Heezik et al. 1994). I conducted a survey of more than 4300 breeding pairs in the colony from 27 February to 1 March 1998 to determine the proportion of early (those brooding a chick) and late (those still incubating an egg) breeders in the periphery and centre of the colony. In king penguins, the distinction between early and late breeders is important because less than 5% of late breeders fledge chicks, compared with more than 50% for early breeders (Weimerskirch et al. 1992; Olsson 1996). Following Ainley et al. (1983), Emslie et al. (1995) and Barbosa et al. (1997), I defined the periphery as the area situated within approximately 2 m of the colony edge. Birds situated more than 2 m from the periphery have at least two or three circles of conspecific neighbours occupying territories in all directions around them and, therefore, are not the first birds to interact with predators attempting to find a passage into the colony (Ainley et al. 1983; Emslie et al. 1995). I estimated that approximately 20% of the colony area was occupied by the periphery, which represented approximately 8000 breeding pairs.

I used 15 min focal animal sampling to study king penguins’ aggressive behaviour (Altman 1974). A total of 178 focal observations were conducted from 26 January to 2 March 1998. Observations covered the complete daylight period, from 0600 to 2100 hours, and were carried out from outside the colony at distances of 10–300 m. I used five different blinds to conduct observations at close range and a × 22 wide-angle spotting scope to observe individuals situated at distances greater than 15 m. Territorial birds were regularly spaced throughout the colony and all focal penguins were occupying a breeding territory adjacent to other territorial birds. The number of neighbours situated at a pecking distance from the focal bird ranged from two to seven (X ± SD = 4.6 ± 1.3, N = 178) and distance between neighbours had a mean ± SD of 49.4 ± 8.9 cm (N = 67). I
conducted 72 (40%) focal observations on birds selected randomly among marked birds. All other focal samples (N=106) were undertaken on unmarked and untouched birds selected randomly in the colony. I used natural features present in the colony and an artificial grid system to ensure that each unmarked bird was sampled once, and that only the male or the female on the same territory was observed. In addition, I did not sample the behaviour of neighbours because data collected from individuals contesting the same boundary are not likely to be independent. In each focal sample, the time of the day, weather and general habitat of the territory (on the beach on level ground or on the sides of the valley with a 10–30° rocky slope) were noted. Because penguins were regularly spaced throughout the colony, the density of territorial breeders was similar in the two habitats. Also, I sampled equivalent numbers of penguins near to and far from the periphery on both the beach and the valley sides. At the beginning of each focal observation, ambient temperature was measured (to the nearest degree) and wind speed assigned as: no wind, light, moderate, strong or very strong. During the focal sample, I recorded all agonistic interactions with neighbours and intruders moving through the territory. I also noted all instances of penguin movements on the territory that did not elicit aggressive behaviour. I estimated visually the distance of the focal bird to the colony edge and to the closest penguin trail to the nearest 0.5 m. Before starting the study and regularly afterwards, I verified my distance estimations with a 1 m ruler.

King penguin activities were classified as: (1) territory defence: aggressive behaviour including beak pointing (no vocalization, beak closed, body stretched out), gaping (pointing but with bill open and vocalizing, body stretched out), pecking and flipper blows (Spurr 1974b; Challet et al. 1994); (2) maintenance: mainly preening but also included stretching, moving and shaking the head, slow and rapid flipper flapping, tail wagging, vocalizing, scratching etc. (Ainley 1974; Challet et al. 1994); (3) rest: standing, bill pointed forward with no head movement (Challet et al. 1994); (4) sleep: with head twisted and beak tucked down underneath a flipper (Buchet et al. 1986); and (5) chick-related behaviour: regurgitating food, preening the chick, singing before feeding, any movements to restrain chick from moving away.

Penguins arriving from and leaving for the ocean do not move randomly into the colony, but seem to use trails just outside the colony for most of their terrestrial movements (Côté & Dewasmes 1999). Because trails are situated mainly on the edges of the colony, distance to colony edge and distance to closest penguin trail were strongly correlated (Spearman’s rank correlation: \( r_s = 0.91 \), N=178, \( P<0.0001 \)). Thus, I only considered distance to colony edge when analysing the effects of territory location on aggressiveness.

Chick size was estimated during focal samples according to the chick’s relative height compared to the parent and to the approximate surface exposed when lying, head underneath the brooding pouch of the parent. I used five classes of relative body size and tested the rationale of these categories by following the growth of 54 chicks of known age. The average age in each of the five categories corresponded closely to the first 5 weeks of life, that is, the period until emancipation from the parent (31–40 days) (Barrat 1976; Weimerskirch et al. 1992; unpublished data). Chicks grow from about 430 g during their first week to 3.2 kg at 5 weeks (Barrat 1976).

During focal observations, I recorded all instances of predators walking within possible pecking distance of the focal individual and noted whether the focal penguin threatened, attacked (physical contact) or ignored the predator. I observed a total of 65 passages of Antarctic and subantarctic giant petrels (Macronectes giganteus and M. halli, respectively), subantarctic skua, Catharacta lombergi, kelp gull, Larus dominicanus, and lesser sheath-bill, Chionis minor, in 33 focal samples (19% of total), none resulting in successful predation.

**Statistical Analyses**

I separated threat displays involving no body contact (i.e. beak pointing and gaping) from aggressive interactions with body contact (pecking and flipper blows) in the analyses because I considered that interactions with body contact were more aggressive than encounters without contact (see also Penney 1968; Spurr 1974b; Jouventin 1982). Focal individuals with six or seven neighbours were grouped in one category of greater than versus equal to six neighbours due to small sample size. Time spent defending the territory was arcsine square-root transformed to meet normality. Rates of threat display and aggressive interactions with body contact were not normal despite transformation, and therefore I used nonparametric tests in the analyses involving these variables. I calculated the proportion of nonterritorial birds walking through a territory that were threatened or attacked by the focal individual, and compared these values to the distance to colony edge. Because number of neighbours affected aggressiveness and varied with distance to colony edge in brooding birds (see Results), I used the Kendall rank partial correlation coefficient, controlling for the number of neighbours, to test the effect of distance to edge on aggressive behaviour (Siegel & Castellan 1988). All other variables were not related to number of neighbours. Statistical procedures followed Sokal & Rohlf (1981) and all probability values were two-tailed, with significance level set at \( \alpha = 0.05 \). Averages are reported with one standard error.

**RESULTS**

About 69% of king penguins on the periphery of the colony were still incubating in late February–early March. Late breeders were thus much more common on the colony edge than in the centre (\( G \) test: \( G_1 = 1027.90, N=4324, P<0.0001 \)). In contrast, only 20% of central birds were incubating at that time, indicating that most central territories were occupied by early breeders. In addition, peripheral penguins had about twice as many interactions with predators (24.4% of 90 focal samples) than...
Ambient temperature and time of day were not related to either proportion of time spent in territory defence (linear regressions: $N=178$, all NS) or rate of aggressive interactions (Spearman’s rank correlations: $N=178$, all NS). Similarly, wind speed did not affect the proportion of time spent in territory defence (ANOVA: $F_{1,173}=0.43$, $P=0.73$) or rate of aggressive interactions (Kruskal–Wallis test: $H_{4}=3.05$, $N=177$, $P=0.38$). No measure of aggressiveness differed between marked and unmarked birds (Mann–Whitney $U$ tests: $N_{1}=73$, $N_{2}=106$, all NS). Therefore, all focal samples were pooled in the following analyses.

Penguins brooding a chick spent 18.7 ± 1.5% of observation time in territorial defence compared with 11.5 ± 1.1% for birds incubating ($t$ test: $t_{174}=-3.74$, $P=0.0002$). Rates of threat display and of aggressive interactions with body contact were also much greater in brooding birds than in incubating birds (Table 1).

The number of neighbours on territories close enough to allow interactions involving body contact did not affect the proportion of time spent in territory defence (ANOVA: $F_{2,78}=0.43$, $P=0.78$), rate of threat displays (Kruskal–Wallis test: $H_{4}=3.35$, $N=81$, $P=0.50$), or rate of aggressive interactions with body contact ($H_{4}=3.13$, $N=81$, $P=0.54$) in incubating birds. For brooding birds, however, those with six or more neighbours spent proportionally more time defending their territory than birds with two neighbours (ANOVA: $F_{4.92}=2.83$, $P=0.03$; Fisher post-hoc least significant difference). Also, the rate of threat displays (Kruskal–Wallis test: $H_{4}=14.85$, $N=97$, $P=0.005$) and the rate of aggressive interactions with body contact ($H_{4}=16.88$, $N=97$, $P=0.002$) increased with number of neighbours in brooding birds.

Distance to colony edge was not related to the proportion of time spent in territory defence (Spearman rank correlation: $r_{5}=-0.08$, $N=81$, $P=0.46$), nor to rates of threat displays ($r_{5}=0.06$, $N=81$, $P=0.57$), or aggressive interactions with body contact ($r_{5}=0.01$, $N=81$, $P=0.92$) in incubating birds. Not surprisingly, penguins in central territories had more neighbours than peripheral birds ($r_{5}=0.21$, $N=97$, $P=0.038$). For this reason, and mainly because the number of neighbours affected aggressiveness of brooding penguins, I controlled for the number of neighbours ($N$) when testing the effect of distance to edge ($E$) on aggressiveness in brooding birds. Proportion of time spent in territory defence ($D$) (Kendall rank partial correlation coefficient: $r_{D.E. N}=0.03$, $N=97$, $P=0.62$) and rate of threat displays ($T$) ($t_{97.1}=0.06$, $N=97$, $P=0.37$) were not affected by distance to edge in brooding birds.

Rate of aggressive interactions with body contact ($B$), however, increased towards the centre of the colony in birds brooding a chick ($t_{97.1}=0.16$, $N=97$, $P=0.017$). In addition, the proportion of intruding penguins attacked when trespassing into the territory of focal individuals increased with distance to edge (Spearman’s rank correlation: incubating birds, $r_{5}=0.28$, $N=60$, $P=0.03$; brooding birds, $r_{5}=0.33$, $N=69$, $P=0.007$; Fig. 1). An alternative explanation could be that central birds are more aggressive than peripheral birds simply because they are less often disturbed by intruders and could therefore invest more time and energy in territory defence. This scenario, however, appears unlikely because the number of intruders did not vary between central and peripheral territories (Mann–Whitney $U$ test: $U=3686.5$, $N_{1}=90$, $N_{2}=88$, $P=0.43$).

Chick age did not affect the proportion of time spent in territory defence (ANOVA: $F_{4.92}=1.82$, $P=0.13$). The rate of threat displays varied significantly with chick age (Kruskal–Wallis test: $H_{4}=10.06$, $N=97$, $P=0.039$) but the rate of aggressive interactions with body contact did not ($H_{4}=5.35$, $N=97$, $P=0.25$; Fig. 2). Parents appeared to point and gape more when the chick was very young (week 1) and just before crèche formation (week 5; Fig. 2). Aggressive interactions with body contact followed the same temporal pattern, although the relationship was not significant (Fig. 2).

Proportion of time spent defending the territory during incubation was not related to breeding date, indicating that early breeders were not more aggressive than late breeders (Spearman’s rank correlation: $r_{5}=-0.18$, $N=34$, $P=0.31$). Also, rate of threat displays ($r_{5}=-0.21$, $N=34$, $P=0.24$) and rate of aggressive interactions with body contact ($r_{5}=0.13$, $N=34$, $P=0.46$) did not vary with breeding date.

Proportion of time spent in territory defence increased with the number of days the bird had spent incubating, both sexes combined ($F_{3.31}=4.99$, $R^{2}=0.14$, $P=0.03$; Fig. 3). On the other hand, I did not find any relation between the rates of aggressive behaviour and the number of days spent incubating (Spearman’s rank correlation: threats: $r_{5}=0.03$, $N=32$, $P=0.88$; aggressive interactions with body contact: $r_{5}=-0.07$, $N=32$, $P=0.71$), indicating that although incubating birds did not interact more often, interactions lasted longer on average towards the end of incubation shifts.

| Table 1. Variation in individual rate of aggressive behaviour (behaviours/h±SE) according to reproductive status in king penguins from Crozet Islands |
|---------------------------------|----------|----------|--------|----------|-----------|
| Threat displays*                | Incubating | 59.0±4.3 | Brooding | 111.8±8.8 | 97 | 2473 | <0.0001 |
| Body contact interactions†      |           | 15.2±4.9 |           | 25.7±4.2 | 97 | 3201 | 0.03   |

*Beak pointing and gaping.
†Pecking and flipper blows.
‡Mann–Whitney $U$ test.
Male and female king penguins spent a similar amount of time in territory defence while incubating (t test: $t_{32}=0.46$, $P=0.65$) and brooding ($t_{36}=-0.55$, $P=0.59$). In addition, they did not differ in rates of aggressive behaviour (Fig. 4).

Incubating penguins occupying territories on the flat beach spent 13.3% of their time in territory defence compared with 9.1% for birds on the sides of the valley (t test: $t_{79}=1.95$, $P=0.05$). Birds incubating on the beach also had a higher rate of aggressive interactions with body contact than birds on territories on the sides of the valley, but did not display more threats (Table 2). Habitat type did not affect the aggressive behaviour of brooding birds. Penguins on the beach and on the sides of the valley spent similar amounts of time in territory defence (t test: $t_{95}=0.65$, $P=0.52$) and had the same rates of threat display and aggressive interactions with body contact while brooding (Table 2).

**DISCUSSION**

In all penguin species but the king penguin (Brodin et al. 1998), the reproductive cycle is completed within 1 year (Williams 1995; Pütz et al. 1998). Although the date of arrival in the colony varies, most adult birds are competing for access to the best territories at approximately the same time (Coulson 1968; Kharitonov & Siegel-Causey 1988; Trivelpiece & Trivelpiece 1990). In king penguins, a pair needs 14–16 months to fledge a chick, thus reproducing early one year precludes early reproduction the following year (Weimerskirch et al. 1992; Olsson 1996). Inevitably, following a successful reproductive episode one year, the pair will either skip a year or breed late the
next year and be very unlikely to fledge a chick (Weimerskirch et al. 1992; van Heezik et al. 1994; Olsson 1996). Therefore, all birds do not necessarily compete in the same period for access to territories because the egg-laying period extends over 4 months. An experienced late breeder, for example, could arrive in the colony when many birds, both experienced and inexperienced, are already hatching their chicks. In my study, early breeders (high reproductive success) occupied most central territories (80%) while late breeders (low reproductive success) occurred mainly on the edges (69%), suggesting that the first birds to arrive chose the central locations and were gradually surrounded by late-arriving pairs. Adélie penguins that move from a peripheral nest to a central nest the following year have a higher breeding success than individuals that stay on the edge, while individuals changing from the centre to the periphery have a lower success than those that remain in the centre (Spurr 1975). Peripheral territories in my study appeared of lesser quality than central territories because chicks on the edges were about twice as susceptible to predator attacks than chicks in central locations (see also Penney 1968; Emslie et al. 1995). Predation is the main cause of mortality in penguin chicks (Taylor 1962; Spurr 1975; Hunter 1991) and Emslie et al. (1995) showed that predation and predation attempts were four to eight times more frequent at colony edges than in the centre in Adélie and Gentoo, Pygoscelis papua, penguin colonies. Furthermore, philopatry appears low in king penguins and cannot explain the choice of territory location. Individuals likely change territories and have different neighbours every year because the divorce rate is very high in king penguins (approximately 80%; Olsson 1998; Bried et al. 1999) and the same birds alternate early and late breeding attempts (Weimerskirch et al. 1992). In such a situation where central territories appear to afford better protection against predators and provide higher breeding success, should experienced but late-arriving birds try to access a central territory by displacing a subordinate bird?

The answer to this is two-fold. First, the territory, regardless of its location, does not have the same value for a bird arriving to breed and one already brooding a chick because the parental investment necessary to replace a chick is much higher than that to replace an egg (Montgomerie & Weatherhead 1988). King penguins that lose their chick cannot replace it during the same year (Weimerskirch et al. 1992). Because the value of the territory is much higher for birds already brooding a chick compared with late-arriving birds, regardless of experience or aggressiveness, brooding birds should be very reluctant to abandon their territory (Spurr 1974a, b; Montgomerie & Weatherhead 1988). The very high level of aggressiveness observed in breeding king penguins (up to 500 interactions per bird per h; Le Maho et al. 1993; Challet et al. 1994) suggests that although fights incur high energetic costs (Hogstad 1987), the benefits of defending a territory must be very high (Montgomerie & Weatherhead 1988). The observed increase in aggressiveness from incubation to brooding (Table 1) can be explained by the higher fitness value of a chick as proposed by parental investment theory (Burger 1981; Siegel-Causey & Hunt 1981; Kilpi 1987; Vinuela et al. 1995; Amat et al. 1996). Similarly, Challet et al. (1994) obtained a three-fold increase in territory defence of king penguins, comparing the incubation and the brooding periods. Chinstrap penguins, Pygoscelis antarctica, also defend chicks more strongly than eggs (Vinuela et al. 1995). There is often a marked behavioural change when a penguin chick hatches, and aggressiveness increases importantly (Spurr 1974a; Derksen 1977). Although the proportion of time spent defending did not change with chick age in king penguins, parents gave more threat displays during the first week after hatching, probably because the chick was very vulnerable at this time (Fig. 2; see also Spurr 1974a; Andersson et al. 1980; Burger 1981;
Burger & Gochfeld 1990). The increase in threat displays observed at the time of côte formation corresponds to the period when the chick reaches its highest fitness value of the guarding phase (Montgomerie & Weatherhead 1988). Also, the increase in aggressiveness with the number of neighbours observed in brooding birds but not in incubating birds indicates the greater propensity of brooding penguins to engage in agonistic behaviours.

Second, based solely on the parental investment theory, there should be no difference in aggressiveness between birds raising a chick in the centre and on the edge of the colony. However, I observed that individuals in the centre (controlling for the number of immediate neighbours) performed more aggressive behaviours towards neighbours than did peripheral birds. This indicates a greater motivation to territory defence in central birds (see also Spurr 1974a, b), even though the proportion of time spent defending the territory was not related to territory location. Individuals in central locations were also more aggressive towards intruders than those on the edges (Fig. 1). Viñuela et al. (1995) reported similar results in chinstrap penguins exposed to human intruders. It would therefore be more difficult for a recently arrived king penguin to displace a central bird than a peripheral one, because the former would be more aggressive towards direct neighbours and intruders than the latter. In addition, a bird arriving would face the attacks of all other territorial breeders while making its way to the centre (Ainley et al. 1983; Côté & Dewasmes 1999). Even if central territories appear more costly to defend in king penguins, it is possible that early breeders select them because they provide the chick better protection against predator attacks and flooding. Finally, aggressiveness did not vary between early and late breeders, indicating that reproductive status (incubating versus brooding) and territory location were the main factors explaining the various levels of aggressiveness observed.

King penguins spent more time in territory defence and the average duration of agonistic behaviours was longer as the number of days spent incubating increased (Fig. 3). The diminution of body reserves during the incubation shift (Cherel et al. 1994) could increase the stress level of a bird and induce higher levels of aggressiveness. In addition, penguins tend to vocalize more towards the end of a shift, a behaviour that normally elicits aggressiveness of neighbours (Stonehouse 1960; Barrat 1976). In their study of video-recorded king penguins, Challet et al. (1994) reported no difference in territory defence between the onset and the end of an incubation shift. However, they monitored only five birds with a recorder operating nine times slower than real time, which might have precluded detection of subtle differences in aggressive behaviour.

As predicted, I did not observe any difference in the aggressive behaviour of male and female king penguins (Fig. 4). On the other hand, male Adélie (Spurr 1974a) and chinstrap (Moreno et al. 1995; Viñuela et al. 1995) penguins are more aggressive than females during pair formation, probably because they have to fend off other males while building a nest and attracting a female. Aggressiveness of males and females does not differ in Adélie penguins following egg laying (Spurr 1974a). However, the situation is different in king penguins because first, they do not build a nest and second, pairs form on the beach and then establish the territory together (Barrat 1976).

During the incubation period, pairs established on the flat beach were more aggressive than those using the sides of the valley, irrespective of distance to colony edge. There were more penguins walking on the beach than on the valley sides and this intense circulation could have induced the higher level of aggressiveness observed. The absence of a relationship between all measures of aggressiveness and habitat type in brooding birds is somehow puzzling. I suggest that the level of aggressiveness observed in brooding birds was too high (average of 19% of time spent in territory defence and 138 aggressive interactions per bird per h) to detect a difference among habitats. Birds raising a chick in both habitats probably reached a threshold of aggressive interactions at which point it became energetically too costly to respond with an increase in aggressiveness (Hogstad 1987).

Aggressiveness increased from incubation to brooding, supporting the parental investment theory. Also, central birds were more aggressive than individuals on the edge of the colony and experienced a higher reproductive success. Aggressiveness of breeders, however, was not directly compared to survival of chicks. To understand fully the relationship between aggressiveness and reproduction in seabirds, further research should follow individually marked animals to measure aggressive behaviour.

Table 2. Effect of habitat type and reproductive status on individual rate of aggressive behaviour (behaviours/h±SE) in breeding king penguins from Crozet Islands

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<tr>
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<th>Beach</th>
<th>Valley sides</th>
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<tr>
<td><strong>Incubating</strong></td>
<td></td>
<td></td>
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<tr>
<td>Threat displays*</td>
<td>15.1±1.3</td>
<td>14.3±1.8</td>
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<tr>
<td>Body contact interactions†</td>
<td>5.1±2.1</td>
<td>1.9±0.5</td>
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<tr>
<td><strong>Brooding</strong></td>
<td></td>
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<tr>
<td>Threat displays*</td>
<td>27.6±3.6</td>
<td>28.0±2.6</td>
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<tr>
<td>Body contact interactions†</td>
<td>7.6±1.7</td>
<td>5.3±1.3</td>
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</tbody>
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*Beak pointing and gaping. †Pecking and flipper blows. ‡Mann–Whitney U test.
and long-term reproductive success according to various territory locations.

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