

ARTICLE

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## Agonistic behavior in wild male Magellanic penguins: when and how do they interact?

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**Abstract** Game-theory models predict that the frequency and type of agonistic interactions should vary with the value of the resource being contested. We describe bill duels and overt fighting in male Magellanic penguins (*Spheniscus magellanicus*) at a breeding colony and determine whether these behaviors change with the value of the nests over which they interact. Bill duels represent low levels of aggression while overt fighting high levels of aggression. Consistent with predictions, overt fighting was more common before egg laying when nests have the highest potential value while bill duels were more common at failed nests later in the season when nests are less valuable as they could not be used for reproduction until the next season. Contrary to expectations, overt fights were shorter and resulted in fewer cuts before egg laying than after egg laying. Large size asymmetries between opponents before egg laying may enable losers to quickly assess their opponents and leave before they are hurt. As predicted, the duration and damage occurring during overt fights were positively correlated with nest cover, which is correlated with higher reproductive success. We conclude that male Magellanic penguins have rules of engagement that in the most cases follow game-theory predictions on when and how to interact.

**Key words** Magellanic penguins · *Spheniscus magellanicus* · Agonistic interactions · Argentina

### Introduction

Models derived from game theory predict that individuals should adjust their behavior to balance the costs of aggression with the value of winning a resource. Individuals should be more aggressive when the potential benefits of winning are high and less aggressive when potential benefits are low (Maynard Smith and Parker 1976; Hammerstein 1981; Parker and Rubenstein 1981; Hammerstein and Parker 1982). Support for these models derives largely from laboratory studies (e.g., Björklund 1989; Smith et al. 1994; Turner 1994; Gabor and Jaeger 1995; Whitehouse 1997) while tests in natural settings are less common (e.g., Robinson 1985; Catterall 1989; Foster 1996; Molina-Borja et al. 1998) even though they are important to determine whether predictions are met in wild populations.

We sought to determine whether these game-theory predictions are met in male Magellanic penguins at a breeding colony. These penguins compete for nests before egg laying, and later in the season, competition continues in failed nests, presumably to acquire ownership for the next breeding season (Renison et al. 2002). The potential value of a nest, measured as the difference in reproductive success between winners and losers, is highest before egg laying, when the nest can be used immediately for reproduction, and lower in failed nests after egg laying, even when controlling for nest cover (Renison 2000; Renison et al. 2002). The potential value of nest sites also varies with the amount of cover: reproductive success is higher in deep burrows with small entrances and lowest in scrapes dug in the soil with no cover (Stokes and Boersma 1998), and hence nests with more cover should be more valuable than those with less cover. Costs of losing include forfeiting nest sites, mates, or mating opportunities and failure to breed (Renison et al. 2002, 2003).

When male Magellanic penguins come into physical contact, they typically use either bill duels or overt fighting (hereafter called fights) (Renison 2000). These behaviors appear to reflect different levels of aggressiveness. Bill duels, by definition, do not involve flipper hits or pecks and

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likely function to provide information about a potential opponent with less risk of damage than fighting. Bill duels developed into fights in 8% of cases (Renison 2000). In fights, one or both opponents incur physical harm (Williams 1995), and male Magellanic penguins are almost always cut with their sharp bills and receive flipper hits during fights (Renison et al. 2002). Fights can last from a few seconds up to 45 min, but most fights were less than a minute. Even short fights usually result in injury. Given that physical harm indicates increased aggression, fights are more aggressive than bill duels. Waas (1990) suggested a similar ranking of aggression in the little blue penguin *Eudyptula minor*. Magellanic penguin fights were mainly between an intruder and an owner (80%) while a few fights were between two intruders (20% Renison 2000).

We used differences in levels of aggression between bill duels and fights to test two specific predictions derived from game theory: (1) male Magellanic penguins should be more aggressive early in the season when the potential value of the nests is higher than in failed nests later in the season; and (2) the level of aggression over nests should depend on nest cover. Behaviors such as fighting are rare in wild Magellanic penguins, but understanding aggression is important because winning or losing a nest site can determine reproductive success and may influence nest and mate choice (Renison et al. 2002, 2003). Moreover, fighting in captive Magellanic penguins is more frequent and can be a problem in breeding programs of this and other species of the genus (J. Tollini, personal communication).

Materials and methods

Study area and general procedures

We recorded bill duels and fights between male Magellanic penguins at Punta Tombo, Argentina (44°02'S, 65°11'W) for four breeding seasons from September 1992 to January 1996 (Table 1). Punta Tombo has the largest colony of Magellanic penguins in the world (over 200,000 breeding pairs). Around 50% of the nests at Punta Tombo are in burrows dug in the soil and the rest are bush nests (Stokes and Boersma 1998). Our study area had approximately 2,000 breeding pairs in an area of relatively high density of nests, which were almost exclusively burrows dug in the soil. Except when specifically mentioned, birds were sexed visually by the depth of their bill, and only male-to-male encounters were analyzed. Visual sexual assignments were 97% accurate, as evidenced by body measurements and

cloaca size of 121 birds we captured after visual estimation (Scolaro et al. 1983; Boersma and Davies 1987).

Measures of aggressiveness

We used two separate measures of aggressiveness: the relative frequency of bill duels and fights and the severity of fights themselves. To determine the relative frequency of encounters, we recorded all bill duels and fights observed. We recorded encounters for 13 h early in the morning and late in the afternoon, the times when penguins were most active (Renison 2000). Bill duels were counted when two birds were seen standing face to face and knocking their bills together (see Boersma 1974; Boersma 1977). Sometimes, bill-duel contests had several bouts (Renison 2000), which were counted as only one bill-duel contest. When bill duels developed into a fight, they were recorded as fights and not as bill duels. Penguins engaged in fighting hit each other with their flippers and pecked at their opponents with their hooked bills. Fighting birds sometimes interlocked bills, pulling or twisting while attempting to hit each other, and fights could also last for several bouts. Bill duels and fights were very distinct behaviors and never occurred simultaneously.

To determine the severity of fights, we quantified their duration, number of flipper hits, and total length of cuts on the bare skin of the face at the base of the bill. Only fights of at least 20 s were scored because shorter interactions were difficult to record accurately. Fights were rare events; hence, we also included six fights that we observed opportunistically. We timed duration from when the birds first made physical contact (the first peck or flipper hit) to when they lost contact, and we added the duration of each bout. We considered the end of a fight to be when either of the opponents left the area or when more than 5 minutes elapsed without contact. We estimated all flipper hits during a fight by watching the opponents and by the sound they produced. Because flipper hits were hard to count, we estimated them in groups of five and could not ascribe hits to each individual. After a fight we captured and flipper-banded both birds, measured each cut to an accuracy of 0.5 cm, and summed the length of cuts on each contestant. Although birds received cuts to other parts of the body, they were most common (and easiest to detect) on the bare skin around the bill and eye, and we included only these cuts in the analysis. We did not count cuts from previous fights. Although rare, they were easily distinguishable from new cuts, as blood soon mixed with soil forming a dirt crust.

**Table 1.** Observation hours recording bill duels and fights, pooled for all study years (1992–1996, *n* = 357 observation periods, 463 h) and grouped by 10-day subsets for analysis

Days of month	September	October	November	December	January	February
1–10	–	22	4	22	48	24
11–20	65	2	24	39	37	11
21–30/1	60	3	23	44	35	–
Total hours	125	27	51	105	120	35

## Indices for benefits of winning

We used two separate indices for the benefits of winning a nest: the period within the breeding season and the cover of the nest where a bill duel or fight occurred. Males arrived at Punta Tombo breeding colony around mid-September. By 21 October, more than 95% of the male penguins were at sea again. Females remained incubating their eggs, and almost no agonistic interactions occurred. In early November, males arrived back, and agonistic interactions were more frequent. Most interactions during this period of the breeding season were near or inside failed nests (for fights 80%; no quantification for bill duels, Renison 2000). We excluded interactions in nests with eggs or chicks because the value of the nest is much higher for the males with progeny but were too few to analyze separately (Renison et al. 2002). Therefore, we classified aggressive contests prior to 21 October as “before egg laying” and those after 21 October in failed nests as “after egg laying.” We considered potential nest value to be greater before egg laying and smaller after egg laying.

As a second measure of the value of winning, we assigned nest-cover scores, as in Stokes and Boersma (1998). Nest-cover scores ranged from “1” (considered the worst) to “5” (considered the best) and were estimated as follows: “1” = egg cup without a roof, side walls less than 30 cm high; “2” = egg cup with side walls 30 cm or higher and a roof that covers less than 50% of the cup; “3” = roof covers 50% or more of the egg cup, but an incubating penguin does not fit entirely under the roof; “4” = egg cup covered 100% from all sides but with a large entrance; and “5” = egg cup covered 100% and a small entrance.

## Statistics

We found no significant differences among breeding seasons in the parameters measured, so we pooled our data for the four study seasons (Table 1). To avoid biasing our samples toward birds that fought frequently, for the analysis of fight severity, we randomly selected only one fight per bird and discarded the other data (as in Renison et al. 2002). Statistics are reported as the mean  $\pm$  SE, and all tests are two tailed.

We used nonparametric tests for analysis, as variables did not have a normal distribution and transformations did not normalize the data. We compared bill duels and fight seen per hour before and after egg laying using Mann–Whitney  $U$  test. Our sampling units were the 357 observation periods, which varied from 1 to 3 h and included a total of 463 observation hours (Table 1). We also compared fight duration, cuts, and flipper hits before and after egg laying using Mann–Whitney  $U$  test. Here our sampling units were the fights longer than 20 s ( $n = 168$  fights; 106 fights before egg laying and 62 fights after egg laying). To compare the cover scores of the nests where birds fought and where they bill dueled, we also used a Mann–Whitney  $U$  test. Here the sampling units were 24 nests where fights occurred and 29 nests where bill duels occurred during the same observation

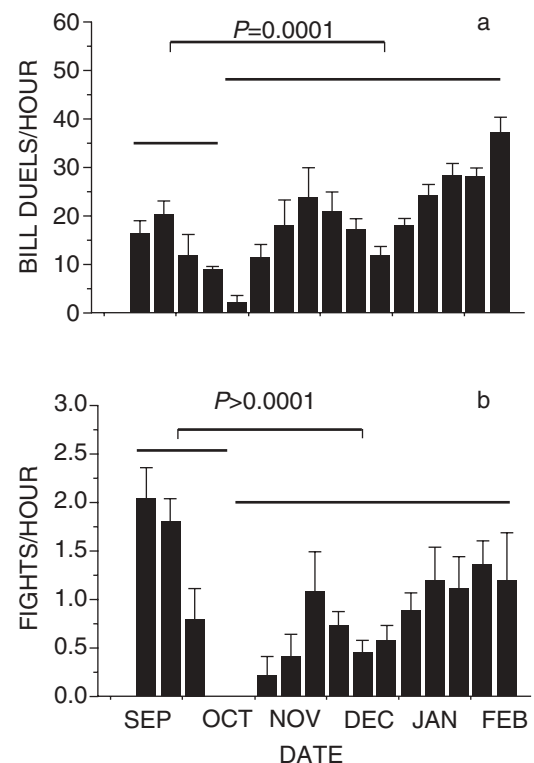
period as a fight. We did not score more nests for this comparison because differences were very evident, and we did not need larger sample sizes. To determine whether fight duration, cuts, and flipper hits were correlated to nest cover scores, we used Spearman rank correlation  $n = 168$  fights). We repeated the correlation for fights before and after egg laying but found no differences and pooled data.

## Results

### Aggressiveness and period of breeding season

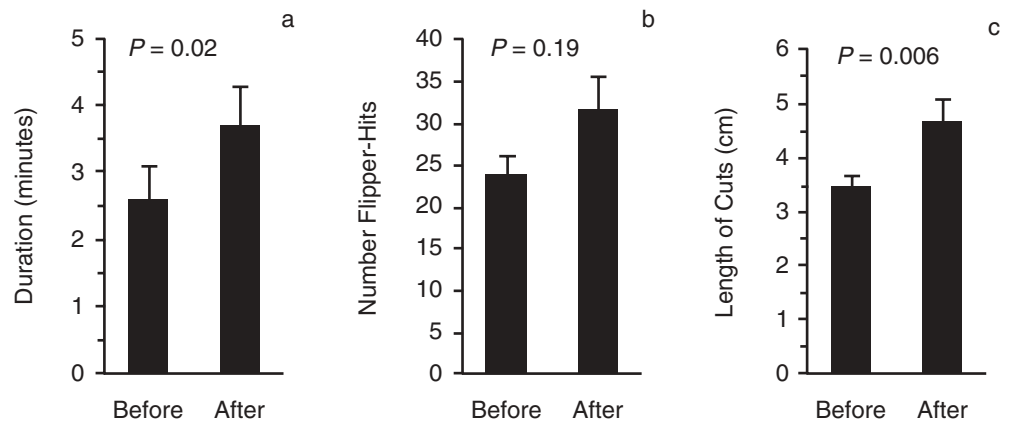
The type and relative frequency of male encounters varied with the period of the breeding season (Fig. 1). Fighting rates were higher before egg laying than after egg laying (Mann–Whitney  $U$  test,  $U = 9,093$ ,  $n = 357$  observation periods,  $P < 0.0001$ ). Bill dueling rates were higher after egg laying than before ( $U = 1,000$ ,  $n = 357$  observation periods,  $P = 0.0001$ ).

Fight duration and damage also changed with the period of the breeding season (Fig. 2). Fight duration was shorter before egg laying than after egg laying (before:  $2.6 \pm 0.5$  min,  $n = 106$  fights; after:  $3.7 \pm 0.6$ ,  $n = 62$ ;  $U$  test,  $U = 2,583$ ,  $P = 0.02$ ). Because fights were shorter before egg laying, not surprisingly, the summed length of cuts was less before egg laying than after egg laying (before:  $3.47 \pm 0.2$  cm; after:  $4.66 \pm 0.4$ ;  $U = 2,465$ ,  $P = 0.006$ ). Number of



**Fig. 1.** Number of bill duels (a) and fights (b) seen per hour during the season. Horizontal lines above the bars indicate the before and after egg-laying periods. Each column represents the average  $\pm$  SE number of behaviors per hour in periods of 10 days (see Table 1)

**Fig. 2.** Mean duration (a), number of flipper hits (b), and length of cuts (c) per fight before and after egg laying ( $\pm$ SE; before:  $n = 106$  fights; after:  $n = 62$  fights)



flipper hits per fight were not significantly different before and after egg laying (before:  $23.9 \pm 2.4$ ; after:  $31.8 \pm 4.0$ ;  $U = 2,889$ ,  $P = 0.19$ ).

#### Aggressiveness and nest cover

Nests where birds fought had more cover (mean cover score  $3.84 \pm 0.24$ ,  $n = 24$  fights) than nests where birds bill dueled (mean cover score  $2.86 \pm 0.25$ ,  $n = 29$  bill duels; Mann-Whitney  $U$  test,  $U = 212$ ,  $P = 0.01$ ). Almost all (96%) of the fights occurred inside a nest while most bill duels (87%) took place in the open area outside the nest. When a bill duel occurred inside a nest, the nest was a hollow without a proper roof or only one of the opponents was inside the nest while the other was outside. We never saw two male penguins entirely inside a well-covered nest except when engaged in a fight.

Fight duration and the summed length of cuts were both positively correlated with nest-cover scores (Spearman rank correlation:  $r_s = 0.23$ ,  $n = 168$ ,  $P = 0.003$ ; and  $r_s = 0.25$ ,  $P = 0.001$ ; respectively). The number of flipper hits, however, was not correlated with nest cover ( $r_s = 0.01$ ,  $P = 0.90$ ).

## Discussion

Resource value is known to affect the type and intensity of agonistic behavior in a large proportion of studied species (Itzkowitz 1979; Powers 1989; Gabor and Jaeger 1995; Hodge and Uetz 1995), and most results from our study in male Magellanic penguins in a natural setting are in coincidence. Fighting, which represents a high level of aggression, occurred more frequently before egg laying when the benefits of winning are higher than after egg laying when the benefits of winning are lower. Before egg laying, penguins are also under a severe time constraint, as breeding is highly synchronized (Boersma et al. 1990), and delays might mean a missed breeding season. Thus, male penguins before egg laying should fight until they obtain or retain their nests.

Males cannot afford as much time early in the season as they can later in the season to evaluate opponents.

After egg laying, the value of a nest is reduced, as failed breeders may not use the nest to breed until the next season (Renison et al. 2002). Our results suggest that failed breeders can afford the time for bill duels to safely evaluate potential opponents, which also explains why Renison et al. (2002) found that when fighting does occur after egg laying, opponents tend to be more equally matched in size compared with opponents before egg laying. As occurs with little blue penguins (Waas 1991), bill duels could be low-intensity aggressive contests, which function to communicate the birds' willingness to defend their nest and the possible outcome of a potential fight. During bill duels, the sharp bills are close to the opponent's head, and birds could easily damage an opponent and engage in a fight, which happens in 8% of the bill duels (Renison 2000). Thus, bill duels may function as a honest signal of willingness to fight, as suggested by Waas (1991) for little blue penguins. Males repeatedly hit each other with the bill, so bill dueling may also allow birds to determine the strength and mass of an opponent.

Seemingly contrary to game-theory expectations, we found that the severity of fights (as measured by duration and length of cuts) was lower before egg laying than after. As male fighters before egg laying are less equally matched in size (Renison et al. 2002), the large size asymmetry before egg laying may allow the loser to quickly determine the better fighter.

As expected, we also found that male Magellanic penguins fought over nests with good cover but bill dueled over low-cover nests. Likewise, Spurr (1974) reported that Adélie penguins (*Pygoscelis adeliae*) in the more-valuable center nests of the colony were more aggressive than individuals in the less-valuable periphery nests. Waas (1990) reported that little blue penguins adapt their aggressive repertoires to the different habitats they live in, suggesting that agonistic behaviors are modified according to costs and benefits. Our data further supports the idea that penguins follow rules for how aggressively they will interact, as fight duration and the summed length of cuts produced during fights were both positively correlated with nest cover.



A correlation between resource quality and duration of aggressive encounter is known for several bird species (Robinson 1985; Brodsky and Montgomerie 1987; Catterall 1989).

We conclude that the level of aggression between male Magellanic penguins tends to correspond with the potential value of the resource they are contesting. Although fights were not always longer and more damaging when nests were of higher value, mild encounters (bill duels) were primarily associated to low-value nests while more aggressive behaviors (fights) were associated with high-value nests. Thus, male Magellanic penguins appear to have rules of engagement, and in a wild, natural setting, they generally follow game-theory predictions for agonistic behavior.

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