

Winning and losing: causes for variability in outcome of fights in male Magellanic penguins (*Spheniscus magellanicus*)

Daniel Renison,^a Dee Boersma,^b and Mónica B. Martella^a

^aCentro de Zoología Aplicada, Universidad Nacional de Córdoba, C.C. 122, 5000 Córdoba, Argentina, and ^bDepartment of Zoology, Box 351800, University of Washington, Seattle, WA 98185, USA

Game theory models predict that fighting ability should be more important in contest outcome when the payoffs of winning are high for both contestants, and ownership should be more important when payoffs are low. Male Magellanic penguins (*Spheniscus magellanicus*) provide an opportunity to test these predictions in a natural setting because payoffs of winning are higher for penguins fighting before egg laying and lower for penguins fighting after egg laying, allowing the prediction of differences in who should win and lose. We watched an area of approximately 2000 Magellanic penguin nests from 1992 to 1996 at Punta Tombo breeding colony, Argentina; we quantified fighting behavior, banded contestants, measured their body size (here used as an index of fighting ability), determined ownership status when possible, and monitored their reproductive success. We determined that male Magellanic penguins fought for nests and mates. As theory predicts, before egg laying, body size difference was more important than ownership as a predictor of contest outcome and fight duration. After egg laying, owners won fights, and size did not predict who won or how long they fought. Our comparisons of nest ownership, nest quality, and chicks fledged by winners and losers suggested that our predictions on the change in benefits of winning before and after egg laying were correct. We conclude that game theory models are useful in predicting who won or lost fights in male Magellanic penguins and that ultimate benefits of winning fights are related to fitness. *Key words*: aggression, fight outcome, fighting, game theory, penguins, *Spheniscus magellanicus*. [*Behav Ecol* 13:462–466 (2002)]

Game theory models suggest that respect of a conventional rule like “owners win” could be an evolutionarily stable strategy (ESS) in dispute resolution when the benefits of winning a fight are low relative to fighting costs (Maynard Smith and Parker, 1976). When payoffs of winning fights are high for at least for one of the contestants, a conventional rule is unlikely to be an ESS because individuals that break the rule would benefit, and models predict that in those cases disputes should be determined by asymmetries in fighting ability (also known as resource-holding potential) or asymmetries in the value of the disputed resources between contestants (Enquist and Leimar, 1983; Leimar and Enquist, 1984; Maynard Smith and Parker, 1976; Parker, 1974). When asymmetries in fighting ability or resource value are used to settle contests, individuals should evaluate these asymmetries during the fight and use this information to determine whether to retreat and avoid further injury or to continue fighting. As a consequence, when differences in fighting ability between contestants are smaller, the probability of victory for the animal with the greater fighting ability should decrease, and fight duration should increase (Enquist and Leimar, 1983; Parker, 1974).

Although many aspects of game theory predictions have been tested, predictions relating the importance of payoffs of fighting on the type of asymmetry used to settle contests have generally been only indirectly supported and very seldom tested. For example, many studies showed that contestants with greater fighting ability win fights in a variety of species where the payoffs of winning are assumed or proven to be high (e.g.,

arthropods: Foster, 1996; fish: Lindström, 1992; Schuett, 1997; amphibians: Davies and Halliday, 1978; Robertson, 1986; reptiles: Molina-Borja et al., 1998; Olsson, 1994; birds: Björklund, 1989; Petrie, 1984; mammals: Clutton-Brock et al., 1979; Haley et al., 1994). Conversely, other studies performed with several bird species where payoffs to the winner are presumably high showed that asymmetries in resource value are important in determining the outcome of fights (e.g., Davies, 1981; Elfström, 1997; Krebs, 1982). Finally, ownership appears to be important in fight outcome in species where payoffs of fighting are low due to high fighting costs (e.g., birds: Nelson, 1984) or because of the low value of the acquired territory (e.g., arthropods: Davies, 1978).

The few studies that explicitly tested the game theory predictions in relation to the importance of fighting payoffs on the type of asymmetry used to settle fights were performed comparing two populations of the same species, with differing costs and benefits associated with fight behavior. Englund and Otto (1991) found ownership more important in a sparse population of *Agrypnia pagetana* (Trichoptera) larvae that fought for cases within which to live, while weight asymmetry was more important in a high-density population where cases were a more valuable resource. Hammerstein and Riechert (1988) compared fighting behavior of two ecotypes of desert spiders *Agelenopsis aperta*. The proportion of strategies used by *A. aperta* could be well predicted by game theory models in a desert grassland habitat. However, in a desert riparian ecotype where payoffs of winning were lower, ownership was not as important in contest settlement as predicted. The authors attributed this discrepancy to gene flow between the two ecotypes, which prevented the riparian ecotype from reaching an ESS that was locally adapted.

In vertebrates, explicit tests of game theory models relating payoffs to who wins fights are still lacking, even though theory is well advanced and has largely been used to explain why owners may win fights over intruders. In this study we tested

Address correspondence to D. Renison. E-mail: drenison@com.uncor.edu.

Received 18 April 2000; revised 22 March 2001; accepted 4 September 2001.

© 2002 International Society for Behavioral Ecology

game theory qualitative predictions for the outcome of individual fights using a single population of breeding male Magellanic penguins (*Spheniscus magellanicus*), where the benefits of winning are expected to change during the breeding season, and hence the type of asymmetry used to settle fights is predicted to change correspondingly. Magellanic penguins fight during most of the breeding season over well-covered nests, which they use for several seasons and which enhances their reproductive success by protecting adults from heat and eggs and chicks from predators (Stokes, 1994; Stokes and Boersma, 1998). The breeding cycle of Magellanic penguins is highly synchronized, and penguins that acquire a nest after egg laying is completed are not able to breed successfully in the disputed nest until the next breeding season (Boersma et al., 1990). We therefore expected the benefits of winning to be highest before egg laying, when having a nest is of immediate importance for reproduction for both contestants, and lower after egg laying when both contestants are not breeding and nests will only be used for the next breeding season.

Our specific goals were to (1) confirm Stokes' (1994) finding that male Magellanic penguins fight for nests and additionally determine whether they also fight for mates; (2) determine if fighting ability is more important than ownership before egg laying and less important after egg laying, as predicted by game theory models; (3) determine if there is a corresponding change in the influence of fighting ability on fight duration: before egg laying, fight duration should be correlated to disparity in fighting ability, but after egg laying we should not find this relationship; and (4) evaluate whether our prediction that the benefits of fighting are lower after egg laying than before egg laying was correct.

METHODS

Study area

We studied Magellanic penguin fights at Punta Tombo, Argentina (44°02' S, 65°11' W) from February 1992 to January 1996. The study area was mainly devoid of vegetation, had a density of 20–30 nests/100 m² (Stokes and Boersma, 2000), and included approximately 2000 nests that were mainly burrows dug in the soil (Renison, 2000).

General procedures

We watched the study area looking for fights for more than 500 h, primarily in the early morning and late afternoon, when the penguins were most active. Fight duration was timed with a chronometer. A fight was considered to start when birds pecked and/or flipper hit each other; it was considered to end when contestants lost contact and one of the contestants left the area or more than 5 min elapsed without further contact. We arbitrarily considered a fight when both contestants pecked or flipper hit each other for 20 s or more.

After a fight, we marked the contested nest, captured both contestants, and banded them with stainless-steel flipper bands. We measured their bill length and depth and flipper and foot length (see Boersma, 1974). Fighters were later sexed by body measurements, patterns of pairing and arrival to the colony, and visual examination of their cloacas (Boersma and Davies, 1987; Scolaro et al., 1983). We later discarded fights with male–female or female–female contestants because we suspected payoffs of fighting for females were lower. We also discarded fights that occurred in nests with eggs or chicks because one of the contestants was usually the parent and resource value asymmetries existed between fighters, and because this class of fights was too few to study separately.

We localized nests where contestants bred by systematically

visiting all nests in the study area once in early October, when most birds were in the colony, and 2–3 times in late October and early November, when breeding males were incubating. Additionally, we searched for contestants less systematically by walking around the area for at least 20 min every 2–8 days during most of the season. Although we may have missed a few birds that lost their eggs early, it is unlikely that we missed birds that fledged chicks.

We marked and checked nests occupied with contestants every 4–15 days during the breeding season. Their chicks were individually marked and considered to have fledged if they were alive after 8 January and their mass was at least 1.8 kg (Boersma et al., 1990). A male was considered the parent of the eggs or chicks in the nest when it was the only male present at the nest 6 days before the eggs were laid or if the male and female were seen consistently at the nest when checked after egg laying. Because extrapair copulations in Magellanic penguins are rare (Hood, 1996), males without an active nest were assumed to have produced no chicks during that season.

We classified fights as occurring before egg laying when they occurred before 20 October, by which date most male penguins were out at sea and females were left to take the first incubation shift (Yorio and Boersma, 1994). Fights after 20 October were classified as after-egg-laying fights.

Causes of fights

We determined if males fought for the best quality nests by comparing nest quality codes of nests where fights occurred with comparison nests. Comparison nests were chosen in the field as the closest nest with no eggs or chicks, occupied by a male with no cuts or blood that was not seen fighting during that season. The nest quality scale ranged from 1 (poorest), for those nests that consisted of a scrape with no roof cover, to 5 (best) for those nests that were well covered, which in the case of our study area were deep burrows with a small entrance (Stokes and Boersma, 1998).

We determined if males fought for mates by comparing female presence in nests where fights occurred and comparison nests of equal quality. Comparison nests were chosen from a map of all study nests as the closest nest of equal quality but with no eggs and occupied by a male with no cuts or blood that was not seen fighting during the season. Most comparison nests were occupied by birds we saw fighting in a previous season, but we do not believe that having fought in a previous season could affect nest attendance of the females in the following season. As female presence can vary with date, we only selected comparison nests that had been checked on a similar date (± 4 days) as the fight nest.

Outcome of fights

We tested the predictions of game theory models on fighting outcome by comparing body size (here used as a measure of fighting ability or resource-holding potential) and ownership status of winners and losers before and after egg laying. We calculated a body size index as the first factor extracted from a principal component analysis of body measurements (Hood et al., 1998; Yorio and Boersma, 1994). We did not use body mass as a measure of size because mass is highly variable, depending largely on how long the bird has been fasting (Fowler et al., 1994). A bird was classified as the nest owner if it was the parent of the eggs laid in the nest during the previous breeding attempt (the previous breeding season for fights before egg laying, and the same breeding season for fights after egg laying).

We determined if larger asymmetries between contestants augmented the probability of the larger penguin being the

Table 1
Number and percentage of male Magellanic penguin owners and intruders that won fights before and after egg laying

	Owners won	Intruders won
Before egg laying	12 (55%)	10 (45%)
After egg laying	15 (88%)	2 (12%)

winner by dividing size differences in six groups and calculating the proportion of larger contestants that won fights within each group. We correlated size asymmetry and fight duration to determine if size asymmetry influenced fight duration.

Benefits of winning

The benefits of winning a fight can be measured as the increase in reproductive success as a result of winning (Grafen, 1987). We quantified how the value of winning changes through the breeding season by comparing three aspects related to reproductive success between winners and losers: nest ownership, nest quality, and number of chicks fledged at the next breeding opportunity (i.e., for fights after egg laying, we measured reproduction success in the next year). If fighting ability and parental quality were tightly linked, this would confound results because, in this case, higher reproductive success would not necessarily result from winning. We determined whether fighting ability and parental quality were associated by comparing breeding success of winners and losers that both had nests of similar quality, and of winners and losers that both lost the disputed nest.

Statistical treatment

We found no significant differences among seasons in all parameters measured, so data from different seasons were pooled for analysis. We used paired statistical comparisons throughout (paired Sign, Wilcoxon, and *t* tests), except when comparing nest quality of contestants (Wilcoxon two-sample test), because many losers did not have a nest and their respective winners were unpaired. For each analysis, to better approximate independence of fights, we randomly deleted both contestants in fights where individuals or nests were repeated. Thus, each analysis was performed with only one fight per individual and nest. Fight duration was log transformed, and Pearson correlation was used to relate size asymmetries to fight duration. We did not have complete information for every fight, so some records were omitted, and sample sizes varied depending on the test. For example, we were unable to record fight duration when we arrived at the fight location after the fight started; we only knew nest ownership status when we had records of contestants in the previous breeding attempt, and nest cover codes were only recorded in the last four seasons. We also did not have reproductive success data for fights that occurred after egg laying in the last season of the study.

RESULTS

Causes of fights

Male Magellanic penguins fought at nests with more cover than comparison nests, both before egg laying (mean contested nests cover code = 4.32 ± 0.09 , comparison nests = 3.49 ± 0.12 , Wilcoxon test: $n = 78$ pairs, $z = -5.09$, $p < .001$) and after egg laying (contested nests = 4.23 ± 0.08 , comparison nests: 3.35 ± 0.13 , $n = 56$ pairs, $z = -1.98$, $p = .05$).

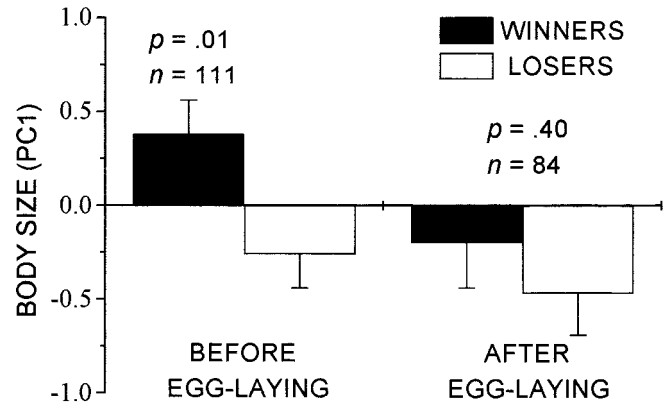


Figure 1
Body size (\pm SE) for winners and losers of male Magellanic penguin fights before and after egg laying.

Before egg laying, female presence was similar in contested and comparison nests (33% in contested nests and 39% in comparison nests of similar quality, Sign test: $n = 81$ pairs, $z = 0.72$, $p = .47$), whereas after egg laying, female presence was higher in contested nests (57% in contested nests and 23% in comparison nests, $n = 44$ pairs, $p = .001$).

Outcome of fights

Before egg laying, nest owners were no more likely to win than intruders (Table 1, chi-square test: $\chi^2 = 0.18$, $df = 1$, $p = .67$), but winners were larger than losers (Figure 1, paired *t* test: $t = 2.74$, $df = 110$, $p = .01$). The larger the body size difference between the contestants, the greater the proportion of larger males who won fights ($r_s = .83$, $n = 6$ size difference ranks, $p = .04$), and the shorter the duration of the fights ($r = -.24$, $n = 97$ fights, $p = .02$).

After egg laying, owners won fights more often than intruders (Table 1, $\chi^2 = 9.94$, $df = 1$, $p = .002$). Body size was similar between winners and losers (Figure 1, paired *t* test: $t = 0.85$, $df = 83$, $p = .40$), and body size was not correlated with the proportion of bigger males who won fights ($r_s = .10$, $n = 6$ size difference ranks, $p = .83$), nor with the duration of fights ($r = -.06$, $n = 65$ fights, $p = .61$).

Benefits of winning fights

For fights before egg laying, 82% of the winners and 40% of losers were found breeding during the season of the fight (Sign test: $n = 111$ fights, $z = 4.16$, $p > .001$). Nest quality of winners was higher than losers (mean = 4.23 ± 0.09 for winners and 3.36 ± 0.15 for losers, $n = 91$ and 44 , $U = 1032$, $p > .0001$). Winners fledged more chicks than losers (mean = 0.42 ± 0.07 chicks/winner and 0.26 ± 0.06 chicks/loser, Wilcoxon test: $n = 111$ fights, $z = -1.92$, $p = .05$). Winners and losers that bred in nests of equal quality had similar reproductive success (mean = 0.75 ± 0.16 chicks/winner and 0.63 ± 0.16 chicks/loser, $n = 24$ fights, $z = -0.66$, $p = .51$). When both contestants lost the nest, their reproductive success was also similar (mean = 0.18 ± 0.09 chicks/winner and 0.30 ± 0.10 chicks/loser, $n = 33$ fights, $z = -0.71$, $p = .48$).

For fights that occurred after egg laying, 61% of the winners and 42% of the losers bred the following season (Sign test: $n = 67$ fights, $z = 2.52$, $p = .01$). However, nest quality and reproductive success did not differ between winners and losers (mean nest quality = 4.24 ± 0.12 for winners and 3.75 ± 0.22 for losers, $n = 41$ and 28 , $U = 446$, $p = .10$; mean reproductive success = 0.36 ± 0.08 chicks/winner and 0.27

± 0.08 chicks/loser, Wilcoxon test: $n = 67$ fights, $z = -0.64$, $p = .52$).

DISCUSSION

Our main results indicated that benefits of winning fights for male Magellanic penguins were higher before egg laying than after egg laying because reproductive success of winners and losers were more similar after egg laying than before egg laying. In agreement with game theory predictions, body size, and not ownership, was an important predictor of fight outcome before egg laying, whereas ownership and not size was important after egg laying.

Before egg laying, more winners than losers were able to breed, usually at better nest sites, and consequently winners fledged more chicks than losers. Acquisition of high-cover nests enhances reproductive success of Magellanic penguins. For example, individuals using nests of low cover fledge 17% fewer chicks per year than those in nests of high cover (Stokes and Boersma, 1998). Victorious contestants could have fledged more chicks because they were better quality parents, not because they won good-quality nests. For example, bigger birds could also be better at rearing chicks and would have fledged more chicks than losers even in bad nests. However, when both contestants ultimately acquired similar quality nests or when both lost the contested nest, reproductive success was similar, which suggests that fighting ability and parental quality are not tightly linked.

Larger contestants were more likely to win in a shorter time, which supports the prediction that fight duration should be correlated to size asymmetry (Enquist and Leimar, 1983). Penguins presumably evaluate the fighting ability of their contestants during the fight, which ends when one of the contestants determines that the other is a better fighter. The loser terminates the fight to avoid further injuries and loss of energy. Saving energy could be important before egg laying because male penguins often stay at the colony, fasting for several weeks (Fowler et al., 1994).

Body size is an important determinant of fight outcome in a large variety of animals (see Archer, 1988 for a list; Foster, 1996; Wells, 1988). In birds, consistent with theory, size has been found to be important in several species where payoffs of fighting are high. For example, in the moorhen (*Gallinula chloropus*), bigger males gain larger territories with more potential nesting sites than smaller males (Petrie, 1984). Likewise, larger yellow-rumped cacique (*Cacique cela*) win more fights and consort with more females than smaller males during the period when eggs are more likely to be fertilized (Robinson, 1985). Our study provides one more example: when payoffs of winning are high, bigger male Magellanic penguins win fights.

Winning fights after egg laying does not have an immediate benefit because penguins cannot breed until the next season. Mates or good-quality nests gained could be lost before the next breeding season begins due to mate loss (Fowler, 1993) or due to burrows collapsing during the winter (Renison et al., personal observations). Our reproductive success data supported our assumption that benefits of winning were lower after egg laying: reproductive success of winners and losers was more similar after egg laying than before egg laying. As predicted by game theory in the situation of fights with low payoffs, we found that winners were mostly nest owners, and size was unimportant in settling contests. Owners have the advantage in contests in several bird species where payoffs of fighting are low, as for example in pigeon guillemots (*Cepphus columba*; Nelson, 1984) and red-winged blackbirds (*Agelaius phoeniceus*; Beletsky and Orians, 1989).

The importance of ownership per se is difficult to assess

because owners can be better fighters (Petrie, 1984), in better condition for fighting (Stutt and Willmer, 1998), or resources can be more valuable to owners (Davies, 1981; Ewald, 1985). Although our study does not escape these difficulties, we believe ownership per se may be relatively more important in male Magellanic penguin fights after egg laying than before egg laying because we excluded fights where one of the contestants had eggs or chicks in their nests, which eliminated cases with obvious resource value asymmetries. Also, after egg laying, no clear value asymmetry between contestants existed, and the index of fighting ability we were able to measure (size) did not explain fight outcome nor duration. The change of asymmetry used to settle contest, from size to ownership, was evident even when many variables that could influence fight outcome could not be controlled, as for example winner-loser effects (Schuett, 1997; Whitehouse, 1997) or information transfer during fights about competitors to non-competitors (Freeman, 1987).

Ownership arguably cannot be used as an arbitrary asymmetry to settle contests in species with long-term territories because individuals that always lose would not breed. This outcome creates a large difference in terms of fitness between winners and losers, a situation that is not evolutionarily stable. In other words, in species with long-term territories, the assumption in Maynard Smith and Parker's (1976) model that each individual has an even chance of winning in future contests is rarely met (Grafen, 1987). However, the temporal pattern of fights in Magellanic penguins is unlikely to create a caste of consistent losers. Under this scenario, nonbreeding birds visit the colony after egg laying and occupy empty nests (Renison et al., personal observations). When owners arrive at their occupied nests, they fight, and ownership is presumably used as a convention to settle fights. However, if a nonbreeding bird does not obtain a nest, it can use its fighting ability to acquire a nest when it returns the next breeding season before egg laying. Maynard Smith and Parker's (1976) second assumption, that contestants do not control fighting costs, is also likely to be met by our study penguins. Once Magellanic penguins start fighting, they almost never revert to less costly aggressive behaviors (Renison, 2000).

The reason for fighting after egg laying may be related to the chances of holding that nest in the following season and attracting a female. This is confirmed by the significantly higher percentage of winners that we found breeding in the following season compared with the losers, even though nest and mate acquisition was not reflected in the reproductive success of the following season. Penguins are known to live for more than two decades, and some individuals remain faithful for more than 14 years to the same nest site; hence small increases in the probability of getting a nest and mate could have lifetime influences on fitness (Stokes and Boersma, 1998) that we could not detect in this study. Possible complementary explanations for fights after egg laying are improving fighting skills and gaining knowledge of the opponent's fighting ability. Because nonbreeding birds cannot invest in their present offspring, even small advantages in this experience investment could be profitable in the future of such a long-lived bird.

We conclude that changes in fitness gains due to acquiring nests before or after egg laying and the associated changes in the type of asymmetry that is important in the outcome and duration of Magellanic penguin fights support qualitative predictions derived from game theory models referring to fight outcomes.

We thank Gisela Giussi, Gustavo Zamora, Julio Vianna, Juliet Rhodes, Federico Tapella, Laura Hood, Andrea Burgos, and Marcela Uhart for helping with field work and/or data entry. Dave Stokes, Ana Cingolani, Brian Walker, Alan Clark, and Guy A. Baldassarre improved

the manuscript. We also thank Steven Beissinger, who read the manuscript and encouraged us to submit it. The field research was funded by Wildlife Conservation Society, USA, and was made possible by a joint agreement between the Society and Organismo Provincial de Turismo of Chubut, Argentina. Data analysis and writing were supported by a doctoral fellowship from Secretaría de Ciencia y Técnica, National University of Córdoba, Argentina, and a research assistantship from the University of Washington and Penguin Fund of Japan. The Centro de Zoología Aplicada, National University of Córdoba, provided working space.

REFERENCES

- Archer J, 1988. The behavioural biology of aggression. Cambridge: Cambridge University Press.
- Beletsky LD, Orians GH, 1989. Territoriality among male red-winged blackbirds III. Testing hypotheses of territorial dominance. *Behav Ecol Sociobiol* 24:333–339.
- Björklund M, 1989. Male contests in the scarlet rosefinch (*Carpodacus erythrinus*) in relation to asymmetries in resource holding power and pairing status. *Behav Ecol Sociobiol* 30:53–58.
- Boersma PD, 1974. Adaptations of the Galapagos penguins for life in two different environments. In: *The biology of the penguin* (B Stonehouse, ed). London: Macmillan; 101–114.
- Boersma PD, Davies EM, 1987. Sexing monomorphic birds by vent measurements. *Auk* 104:779–783.
- Boersma PD, Stokes DL, Yorio PM, 1990. Reproductive variability and historical change of Magellanic penguins (*Spheniscus magellanicus*) at Punta Tombo, Argentina. In: *Penguin biology* (Davis LS, Darby JT, eds). San Diego, California: Academic Press; 15–43.
- Clutton-Brock TH, Albon SD, Gibson RM, Guinness FE, 1979. The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim Behav* 27:211–225.
- Davies NB, 1978. Territorial defence in the speckled wood butterfly (*Pararge aegeria*): the resident always wins. *Anim Behav* 26:138–147.
- Davies NB, 1981. Calling as an ownership convention on pied wagtail territories. *Anim Behav* 29:529–534.
- Davies NB, Halliday TR, 1978. Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature* 274:683–685.
- Elfström ST, 1997. Fighting behaviour and strategy of rock pipit, *Anthus petrosus*, neighbours: cooperative defence. *Anim Behav* 54:535–542.
- Englund G, Otto C, 1991. Effects of ownership status, weight asymmetry, and case fit on the outcome of case contests in two populations of *Agrypnia pagetana* (Trichoptera: Phryganeidae) larvae. *Behav Ecol Sociobiol* 29:113–120.
- Enquist M, Leimar O, 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. *J Theor Biol* 102:387–410.
- Ewald PW, 1985. Influence of asymmetries in resource quality and age on aggression and dominance in black-chinned hummingbirds. *Anim Behav* 33:705–719.
- Foster WA, 1996. Duelling aphids: intraspecific fighting in *Astegopteryx minuta* (Homoptera: Hormaphididae). *Anim Behav* 51:645–655.
- Fowler GS, 1993. Ecological and endocrinological aspects of long-term pair bonds in the Magellanic penguin (*Spheniscus magellanicus*) (PhD thesis). Seattle: University of Washington.
- Fowler GS, Wingfield JC, Boersma PD, Sosa RA, 1994. Reproductive endocrinology and weight change in relation to reproductive success in the Magellanic penguin (*Spheniscus magellanicus*). *Gen Comp Endocrinol* 94:305–315.
- Freeman S, 1987. Male red-winged blackbirds (*Agelaius phoeniceus*) assess the RHP of neighbors by watching contests. *Behav Ecol Sociobiol* 21:307–311.
- Grafen A, 1987. The logic of divisively asymmetric contests: respect for ownership and the desperado effect. *Anim Behav* 35:462–467.
- Haley MP, Deutsch CJ, Le Boeuf BJ, 1994. Size, dominance and copulatory success in male northern elephant seals, *Mirounga angustirostris*. *Anim Behav* 48:1249–1260.
- Hammerstein P, Riechert SE, 1988. Payoffs and strategies in territorial contests: ESS analyses of two ecotypes of the spider *Agelenopsis aperta*. *Evol Ecol* 2:115–138.
- Hood LC, 1996. Adrenocortical response to stress in incubating Magellanic penguins (*Spheniscus magellanicus*) and mate switching in Magellanic penguins at Punta Tombo, Argentina. (MS thesis). Seattle: University of Washington.
- Hood LC, Boersma PD, Wingfield JC, 1998. The adrenocortical response to stress in incubating Magellanic penguins (*Spheniscus magellanicus*). *Auk* 115:76–84.
- Krebs JR, 1982. Territorial defense in the great tit (*Parus major*): do residents always win? *Behav Ecol Sociobiol* 11:185–194.
- Leimar O, Enquist M, 1984. Effects of asymmetries in owner-intruder conflicts. *J Theor Biol* 111:475–491.
- Lindström K, 1992. The effect of resource holding potential, nest size and information about resource quality on the outcome of intruder-owner conflicts in the sand goby. *Behav Ecol Sociobiol* 30:53–58.
- Maynard Smith J, Parker GA, 1976. The logic of asymmetric contests. *Anim Behav* 24:159–175.
- Molina-Borja M, Padron-Fumero M, Alfonso-Martín T, 1998. Morphological and behavioural traits affecting the intensity and outcome of male contests in *Gallotia galloti galloti* (family Lacertidae). *Ethology* 104:314–322.
- Nelson DA, 1984. Communication of intentions in agonistic contexts by the pigeon guillemot, *Cephus columba*. *Behaviour* 88:145–187.
- Olsson M, 1994. Nuptial coloration in the sand lizard, *Lacerta agilis*: an intra-sexually selected cue to fighting ability. *Anim Behav* 48:607–613.
- Parker GA, 1974. Assessment strategy and the evolution of animal conflicts. *J Theor Biol* 47:223–243.
- Petrie M, 1984. Territory size in the moorhen (*Gallinula chloropus*): an outcome of RHP asymmetry between neighbours. *Anim Behav* 32:861–870.
- Renison D, 2000. Comportamiento agresivo en el pingüino de Magallanes (*Spheniscus magellanicus*): un enfoque ecológico (PhD thesis). Córdoba, Argentina: University of Córdoba.
- Robertson JGM, 1986. Male territoriality, fighting and assessment of fighting ability in the Australian frog *Uperoleia rugosa*. *Anim Behav* 34:763–772.
- Robinson SK, 1985. Fighting and assessment in the yellow-rumped cacique (*Cacicus cela*). *Behav Ecol Sociobiol* 18:39–44.
- Schuett GW, 1997. Body size and agonistic experience affect dominance and mating success in male copperheads. *Anim Behav* 54:213–224.
- Scolaro JA, Hall MA, Ximenez IM, 1983. The Magellanic penguin (*Spheniscus magellanicus*): sexing adults by discriminant analysis of morphometric characters. *Auk* 100:221–224.
- Stokes DL, 1994. Nesting habitat use, value, and selection in the Magellanic penguin (*Spheniscus magellanicus*) (PhD thesis). Seattle: University of Washington.
- Stokes DL, Boersma PD, 1998. Nest-site characteristics and reproductive success in Magellanic penguins (*Spheniscus magellanicus*). *Auk* 115:34–49.
- Stokes DL, Boersma PD, 2000. Nesting density and reproductive success in a colonial seabird, the Magellanic penguin. *Ecology* 81:2878–2891.
- Stutt AD, Willmer P, 1998. Territorial defence in speckled wood butterflies: do the hottest males always win? *Anim Behav* 55:1341–1347.
- Wells MS, 1988. Effects of body size and resource value on fighting behaviour in a jumping spider. *Anim Behav* 36:321–326.
- Whitehouse MEA, 1997. Experience influences male-male contests in the spider *Argyrodes antipodiana*. (Theridiidae: Araneae). *Anim Behav* 53:913–923.
- Yorio PM, Boersma PD, 1994. Causes of nest desertion during incubation in the Magellanic penguin (*Spheniscus magellanicus*). *Condor* 96:1076–1083.