

Fighting and assessment in the yellow-rumped cacique (*Cacicus cela*)

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Summary. I tested the prediction derived from game theory models that the intensity of aggressive interactions should reflect the value of the resource being contested and the disparity in fighting ability of the contestants. Females of the yellow-rumped cacique compete for nest sites and the material to build nests. Females competing for established nest sites engage in higher intensity interactions than those competing for sites in which building has not begun and against females robbing nest material (Fig. 1). For males, access to females is determined by dominance, which is positively correlated with weight. Comparably-sized males (Fig. 2) and those of similar rank (Fig. 3) engage in significantly more intense interactions than males that differ widely in size or rank.

Introduction

Competition for limiting resources often involves aggressive interactions between individuals. Game theory models (Maynard Smith and Parker 1976; Hammerstein 1981; Parker and Rubenstein 1981) predict that the intensity of such aggressive interactions should be determined by the value of the resource being contested and the disparity in fighting ability of the contestants. Individuals should fight more intensively for valuable resources, and evenly-matched individuals should fight longer than unevenly-matched contestants. An individual should therefore assess both resource value and the costs involved in the contest for that resource (Maynard Smith and Parker 1976; Hammerstein 1981; Parker and Rubenstein 1981). Empirical

support for these qualitative predictions has come from experimental manipulations of resources and contestants in spiders (Riechert 1978, 1979, 1984), birds (Yasukawa and Bick 1983), insects (Sigursjondottir and Parker 1981; Thornhill 1984; Otronen 1984) and fishes (Rubenstein 1981). There is, however, little evidence from unmanipulated natural populations, largely because resource value and fighting abilities are difficult to measure (but see Petrie 1984). The purpose of this paper is to test whether aggressive interactions in an unmanipulated color-marked population of a bird, the yellow-rumped cacique, follow the predictions of game theory models. First I test the prediction that the intensity of aggressive interactions between females is determined by the value of the resources being contested. And second, I test the prediction that the intensity and duration of aggressive interactions between males should reflect differences in their fighting ability, which in the cacique is determined largely by weight.

Methods

Yellow-rumped caciques (Icterinae: *Cacicus cela*) were studied at the Cocha Cashu Biological Station in the Manu National Park, Department of Madre de Dios, Peru at 71°19'W, 11°51'S. The biological station is located on an oxbow lake (Cocha Cashu) of the Manu River, and is surrounded by undisturbed lowland floodplain forest. Terborgh (1983) provides a detailed account of the climate and vegetation of the Cocha Cashu area. Most caciques nest colonially along the margins of oxbow lakes in low shrubby vegetation in marshes and on islands (Robinson 1985a). Colony size ranges from 2 to 250 nests of which as many as 100 may be active at any one time. Usually, there are between 40 and 100 active nests in the Cocha Cashu area at any one time. Caciques breed from July through February in southeastern Peru (Robinson 1985a). The safest nest sites are in dense clusters on islands, which provide protection against arboreal mammals, snakes and avian predators (Robinson 1985a). Caciques have a polygynous mating system in which males sequentially consort and guard females during the

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period when eggs are laid (Robinson 1985b). Females build the nest, and incubate and feed young with no help from males. Colonies are also the sites of male sexual display and aggressive interactions (Feekees 1981; Robinson 1985b).

I studied caciques for a total of 23 months during the breeding seasons of 1979 to 1983. Birds were individually marked with color bands. During the 5 years of the study, I marked over 700 different caciques. Over 90% of the breeding caciques on Cocha Cashu were color-marked by the middle of the 1981 breeding season.

I visited each active colony on Cocha Cashu once a day. During 2-h periods of observation at large (>40 nest) colonies and 1-h periods at smaller colonies, I recorded data on aggressive interactions among males and females. In this paper, I only consider aggressive encounters between 2 individuals in which both showed behavior that could be rated as aggressive at the beginning of the encounter. The following acts were rated as aggressive: hovering in the air while facing each other less than 20 cm apart, grappling in mid-air, and "shouting" matches in which birds that had disengaged after a grappling fight continued loudly calling while facing each other 10–50 m apart. I deliberately excluded supplants in which only 1 individual acted aggressively. For each interaction, I noted where in the colony it originated, which individuals were involved, which initiated the encounter, and I described the behavior patterns that occurred and the sequence in which they occurred.

I weighed all captured males and recorded time of capture. I only use weights of birds captured within 3 h of dawn to minimize the effects of recent feeding bouts on weight. Consecutive weights from the same male captured on different dates from August through December do not differ significantly (Paired *t*-test, $t=0.94$, $P>0.30$, $n=61$). For this reason, I used weights from males captured at any time during the period from August through December.

Results

Escalation and resource value in females

In this section I examine the kinds and the context of aggressive interactions between females. I arbitrarily distinguished among four sequential levels of increasing intensity in aggressive encounters between two females. In the first level (I), one female flew directly at another and both females hovered in mid-air while facing each other 2–20 cm apart. In Level II both females spiraled downwards without grappling in what appeared to be maneuvering for position. In the third level of intensity, females actually grappled with each other in mid-air (Level III) and began to spiral downwards while locked together. During these grappling fights, the females grabbed each other on the legs and wings, and by the feathers of the breast while they pecked each other on the head. Usually Level III fights were broken off in mid-air and both females returned to the colony. In extreme Level IV cases, however, the fights did not break off until both females hit the foliage, ground, or water below the colony. These were by far the most dangerous fights because females in the water were temporarily

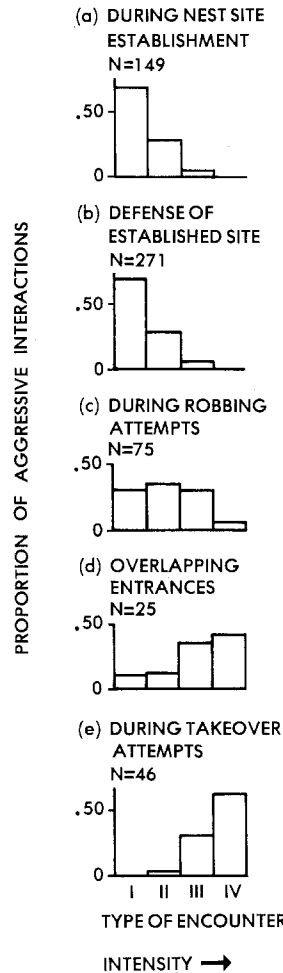


Fig. 1. Levels of escalation of aggressive interactions between females in different contexts. Type I and II encounters did not involve physical contact. Type III and IV encounters involved grappling fights that were often repeated several times. I counted consecutive interactions between the same two individuals in the same day as a single encounter and used the highest level of aggression reached to characterize the intensity of the encounter.

ly helpless and therefore vulnerable to aquatic predators such as black caimans (*Melanosuchus niger*). One female broke her wing during a Level IV fight, probably when she crashed into the foliage under the colony. She then fell into the water where she was immediately eaten by a caiman. Females that escalated to Level III or IV often fought many times in succession before one female departed. During a 1-h period 2 females escalated to a Level III or IV fight 16 times. In between each fight, the females faced each other and erected the feathers of their lower back. After each aggressive encounter, there was usually no clear dominant or subordinate.

There were 5 situations in which females com-

monly interacted aggressively with other females (Fig. 1). The first situation occurred when a group of females settled on a branch in a colony and the females engaged in low intensity (Level I and II) encounters among themselves (Fig. 1a). These encounters occurred before females started building nests and may serve as the means by which the individuals in a group sort out where each will nest on a particular branch. About 64% (145 of 226) of all groups that were begun were abandoned before nests were built.

The second situation occurred when a newly arrived female tried to initiate a nest in the midst of an established group. This attempt can be challenged by the females that have already begun building in that group. Incubating females also sometimes flew out and chased away new females that perched near their nests. These aggressive encounters were of intermediate intensity with about half the interactions involving physical contact (Levels III and IV) (Fig. 1b).

A third situation arose when one female tried to rob nest material from another. Such robberies usually occurred when the nest owner was away. If she returned and discovered the robber, she usually chased her away. However, sometimes, one female tried to rob material from a female as she was holding the material or weaving it into her nest. In these situations, the female being robbed usually challenged the robber and there was a low-intensity encounter or series of encounters (Fig. 1c). Interestingly, some females clearly emerged as winners in these encounters. One female was able to rob 6 other females in her group without any retaliation on the part of the females being robbed. Another female was robbed as soon as she returned to the colony by 7 different females.

The fourth situation in which females interacted aggressively occurred when one female built a nest that covered the entrance of another (Fig. 1d). It is clearly to a female's disadvantage to have her nest entrance woven shut. A female that had her nest sewn shut by another female had to tear a new hole in the side of the nest. Nests with entrances in the side were extremely vulnerable to predators and to harassment by other ceciques (Robinson 1985a, c). In some cases, the offending female shifted her nest to a side of the other female's nest entrance after a brief aggressive encounter. However, in very dense nest clusters there was often little room for such a shift and the dispute was only settled after an intense fight (Fig. 1d). In this situation, both females were defending established nests, and both had much to lose.

The fifth situation in which females interacted aggressively arose when one female tried to take over the nest site of another. All takeover attempts occurred during the first 6 d of building, usually in groups in which nest construction was underway. Takeover attempts were usually directed at nests being built in sites that offered the best protection against predators (Robinson 1985a, d). Aggressive interactions during takeover attempts were intense (Fig. 1e) and could last for hours, though most were settled within 10 min. Unlike most situations in which females interacted aggressively, there was always an easily discernible winner and loser in takeover attempts. The winning female occupied the nest after the fight and the loser either left the Cocha Cashu area (35% of 46 females), tried to establish a new site in the same branch at a later date (30% of 46 females), or switched to another site, usually one that was more exposed to predators (35% of 46 females). Displaced females needed an average of $18.2 \text{ d} \pm 2.8 \text{ (SE)}$ ($n = 30$) to establish a new nest site. Thus, females that were supplanted from a nest site lost time and often lost the opportunity to breed in a safe site. Established nest sites may have also taken less time to complete, because the nests were already partially built.

In summary, all aggressive encounters involved competition for nest sites or the material used to build nests. The intensity of encounters were determined by the value of the resource being contested. Females competing for sites in which building had not yet begun and those competing for nest material had little to gain or lose and tended to engage in low intensity interactions (Figs. 1a–c). Females competing for partially built nests and those competing for space in which to finish nests engaged in high-intensity interactions (Figs. 1d, e). Significantly more encounters between females defending established nest sites escalated to grappling fights (Levels III and IV) than encounters between females defending sites on which building had not yet begun ($\chi^2 = 122.4$, $P \ll 0.001$). Similarly, females competing for established nest sites were significantly more likely to escalate to grappling fights than those competing for nest material ($\chi^2 = 76.0$, $P \ll 0.001$). These results are consistent with the prediction that females assess resource value.

Escalation and disparities in fighting ability among males

Males reached adult size in their third year and only then did they begin interacting aggressively at colony sites where females were building nests

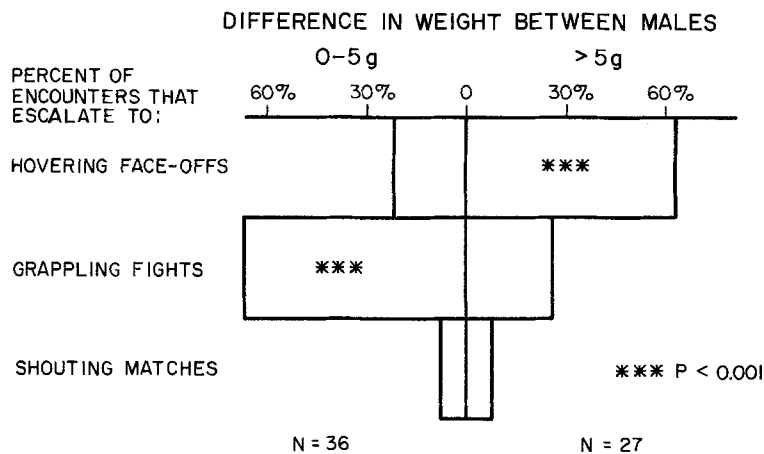


Fig. 2. Differences in weight versus escalation of aggressive encounters between males. All weights were from males captured within 3-h of dawn from August through November

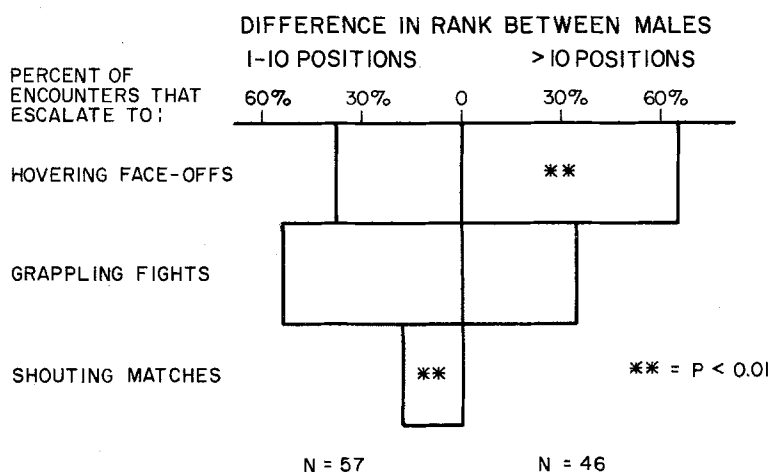


Fig. 3. Difference in rank versus escalation of aggressive encounters between males. Number of "positions" separating males represents the number of males that were dominant to one, but subordinate to the other member of an interacting pair

(Robinson 1985b). When a new male arrived at a colony, he engaged in a series of aggressive interactions in which he attacked or was attacked by males that were already established in that colony. These interactions usually began with an aerial, hovering face-off. Over half (76 of 146) of these aggressive interactions were broken off at this point. The next level of aggression involved an aerial grappling bout in which both birds spiraled downwards. About 40% (58 of 146) of all aggressive interactions ended after a brief grappling bout. Sometimes both birds hit the water or vegetation under a colony. I once saw 2 birds fall right into the jaws of a black caiman under the colony. One male escaped, but the other was eaten. If the encounter did not end after a grappling bout, males then flew away from the colony, perched and shouted at each other for up to 10 min. During these vocal face-offs, the contestants were usually 10 to 50 m apart. Only 11 of 146 interactions in 1982 reached this level of intensity. On at least two occasions, males again grappled with each other after these shouting matches. Aggressive en-

counters among males thus involved a pattern of faceoff-fight-faceoff-fight which could be settled at any level.

The outcome of each aggressive interaction was a clear winner and loser. The winning male could supplant the loser from anywhere within a colony. This dominance was absolute – if A was dominant to B, he was always dominant. From a table of wins and losses for each pair of males in a colony, I could construct a conventional dominance hierarchy that was roughly linear (Robinson 1985b). Dominance was strongly correlated with weight – males in the top half of the hierarchy averaged significantly ($P < 0.001$) heavier than those in the bottom half (Robinson 1985b). The major payoff of dominance was that high-ranking males consorted females during the period when eggs were most likely to be fertilized (Robinson 1985b).

As predicted by game-theory models, encounters between comparably-sized males were more likely to escalate to fights than those between males of different weights (Fig. 2: $\chi^2 = 11.7$, $P < 0.01$). When the disparities in weights were large,

most encounters ended before there was physical contact. Alternatively, males may have used relative position occupied within a colony to assess each other. High-ranking males sang in the center of clusters of nest-building females, while low-ranking males sang from more peripheral positions (Robinson 1985b). Dominant males could attack whichever male was singing from the center of the colony, while lower-ranking males could avoid central males and attack peripheral males. Encounters between closely-ranked males were significantly more likely to escalate to fights than those between distantly-ranked males (Fig. 3: $\chi^2 = 18.3$, $P < 0.001$). However, because dominance and weight were so strongly correlated, it was difficult to determine whether males were using size or position to assess each other.

Discussion

These results are consistent with the prediction that the intensity of a fight should reflect the value of the resource being contested and the disparity in fighting ability between contestants (Maynard Smith and Parker 1976; Hammerstein 1981; Parker and Rubenstein 1981). Females competing for partially-completed nests fought more intensively than those competing for sites in which building has not yet begun or for single pieces of nest material. Partially-completed nests are a valuable resource because they take less time to build, and they are usually in sites that are safe from predators (Robinson 1985a). The costs of losing a takeover attempt involve a loss of both time and opportunity to escape nest predation. Rand and Rand (1976) found that iguanas compete more intensively in contests for deeper, nearly completed burrows than they do for shallow burrows. Riechert (1979) also found that web site quality correlates with a tendency to escalate in the spider *Agelenopsis aperta*. In both iguanas and spiders, however, only the owner of the site knows the true value of that site. In the cacique, nests are exposed and both contestants should know the stage of building and the general vulnerability of a site to predators. In fact, when a long-term resident challenges a newcomer to a population, it is possible that the challenger may know more about the value of the nest site than the nest site owner. Otronen (1984) also found that male flies (*Drosophila anilis*) compete more aggressively for females than for territories, which are only valuable because they attract females.

Escalation between males, on the other hand, appears to be related largely to differences in fight-

ing ability, or "resource holding potential" (Parker 1974), among contestants. Comparably-sized males are more likely to escalate to grappling fights than males that differ widely in weight. Likewise, comparably-ranked males escalate more than widely-ranked males. Under experimental conditions, Rubenstein (1981) showed that by manipulating asymmetries in fighting abilities, he could change the intensity of aggressive interactions in pygmy sunfish (*Elassoma evergladei*). Closely-matched individuals have been shown to interact more aggressively under experimental conditions in blue gourami (*Trichogaster trichopterus*) (Frey and Miller 1972), bluegill sunfish (*Lepomis macrochirus*) (Henderson and Chiszar 1977), stone crabs (*Menippe mercenaria*) (Sinclair 1977), dark-eyed juncos (*Junco hyemalis*) (Yasukawa and Bick 1983), and the spider *Agelenopsis aperta* (Riechert 1978, 1979). Clutton-Brock and Albon (1979) also found that red deer (*Cervus elaphus*) males that were conspicuously different in size seldom fought. Aggressive encounters observed in the field in dark-eyed juncos also tend to involve individuals that are similar in rank (Ketterson 1979) and plumage (Balph et al. 1979). In *Harpobittacus* scorpionflies, Thornhill (1984) found that individuals assess each other during fights, and that as asymmetries in the size of contestants increased, fight intensity decreased.

An interesting feature of aggressive interactions among males is the apparent existence of two stages of assessment during which males face each other but do not fight. If a grappling fight does not settle the outcome, males then engage in shouting matches, which can again escalate to grappling fights. Thus, the escalation sequence of caciques follows essentially the reverse pattern of that reported in red deer (Clutton-Brock and Albon 1979). Instead of beginning encounters with roaring bouts and then escalating to fights as in red deer, many interactions among caciques begin with a brief fight and then switch to a shouting match only if the outcome is still uncertain. Possibly, grappling fights are less costly to caciques than comparable fights are to red deer, though I have seen at least one cacique die as a result of a fight (Robinson 1985b).

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References

- Balph MH, Balph DF, Romesburg HC (1979) Social status signaling in winter flocking birds: an examination of a current hypothesis. *Auk* 96:78–93
- Clutton-Brock TH, Albon SD (1979) The roaring of red deer and the evolution of honest advertisement. *Behaviour* 69:145–170
- Feekes F (1981) Biology and colonial organization of two sympatric caciques, *Cacicus c. cela* and *Cacicus h. haemorrhous* (Icteridae: Aves) in Surinam. *Ardea* 69:83–107
- Frey DF, Miller RJ (1972) The establishment of dominance relationships in the blue gourami *Trichogaster trichopterus* (Pallas). *Behaviour* 42:8–62
- Hammerstein P (1981) The role of asymmetries in animal contests. *Anim Behav* 29:193–205
- Henderson DC, Chiszar DA (1977) Analysis of aggressive behaviour in the bluegill sunfish (*Lepomis macrochirus* Rafinesque): Effects of sex and size. *Anim Behav* 25:122–130
- Ketterson ED (1979) Status signaling in dark-eyed juncos. *Auk* 96:94–99
- Maynard Smith J, Parker GA (1976) The logic of asymmetric contests. *Anim Behav* 24:159–175
- Otronen M (1984) Male contests for territories and females in the fly *Dryomyza anilis*. *Anim Behav* 32:891–898
- Parker GA (1974) Assessment strategy and the evolution of fighting behavior. *J Theor Biol* 47:223–243
- Parker GA, Rubenstein DI (1981) Role assessment, reserve strategy, and acquisition of information in asymmetric animal conflicts. *Anim Behav* 29:221–240
- Petrie M (1984) Territory size in the moorhen (*Gallinula chloropus*): an outcome of RHP asymmetry between neighbours. *Anim Behav* 32:861–870
- Rand AS, Rand WM (1976) Agonistic behaviour in nesting Iguanas: A stochastic analysis of dispute settlement dominated by the minimization of energetic costs. *Z Tierpsychol* 40:279–299
- Riechert SE (1978) Games spiders play: Behavioral variability in territorial disputes. *Behav Ecol Sociobiol* 3:135–162
- Riechert SE (1979) Games spiders play II: Resource assessment strategies. *Behav Ecol Sociobiol* 6:121–128
- Riechert SE (1984) Games spiders play III: Cues underlying context-associated changes in agonistic behaviour. *Anim Behav* 32:1–15
- Robinson SK (1984) Social behavior and sexual selection in a neotropical oriole. PhD thesis, Princeton University, Princeton, NJ
- Robinson SK (1985a) (in press) Coloniality as a defense against nest predators of the Yellow-rumped Cacique. *Auk* 102
- Robinson SK (1985b) (in press) The benefits, costs and determinants of dominance in a neotropical oriole. *Anim Behav* 33
- Robinson SK (1985c) The yellow-rumped cacique and its associated nest pirates. In: Buckley PA, Foster MS, Morton ES, Ridgely RS, Buckley FG (eds) *Neotropical ornithology*. Ornithological Monograph, vol. 36. American Ornithological Union, Washington, DC, pp 898–907
- Robinson SK (1985d) (in press) Competitive and mutualistic interactions between females of a neotropical oriole. *Anim Behav* 33
- Rubenstein DI (1981) Combat and communication in the Everglades pygmy sunfish. *Anim Behav* 29:249–258
- Sigurjonsdottir H, Parker GA (1981) Dung fly struggles: Evidence for assessment strategy. *Behav Ecol Sociobiol* 8:219–230
- Sinclair ME (1977) Agonistic behaviour of the stone crab, *Menippe mercenaria* (Say). *Anim Behav* 25:193–207
- Terborgh JW (1983) Five new world primates: a study in comparative ecology. Monographs in behavior and ecology, vol 1 Princeton University Press, Princeton, NJ
- Thornhill R (1984) Fighting and assessment in *Harpobittacus* scorpionflies. *Evol* 38:204–214
- Yasukawa K, Bick EI (1983) Dominance hierarchies in dark-eyed juncos (*Junco hyemalis*): a test of a game-theory model. *Anim Behav* 31:439–448