Interspecific territoriality of northern harriers: the role of kleptoparasitism

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Abstract. Territorial female northern harriers, *Circus cyaneus*, often evicted species of intruding raptors larger than themselves from their territories, but never species smaller than themselves. Contrary to the hypothesis that aggressive responses serve primarily to reduce exploitative competition, responses by harriers to larger raptor species seldom occurred during hunts by these intruders. However, harriers responded frequently to larger raptor species when these species intruded while harriers were actively hunting, supporting the hypothesis that aggressive responses serve primarily to reduce interference competition in the form of kleptoparasitism of harriers’ prey by larger raptor species. The lack of defence by harriers against smaller intruding raptor species apparently resulted from harriers’ abilities to kleptoparasitize these intruders. Hence, whether or not a territorial harrier responded aggressively to an intruding raptor species depended on the size of the harrier relative to the size of the intruder, which in turn influenced its ability to kleptoparasitize or to be kleptoparasitized.

Many animals defend territories against individuals of other species (heterospecifics) in addition to individuals of their own species. Interspecific territoriality is attributed most often to the defence of food supplies, shelters and/or breeding sites (e.g. Orians & Willson 1964; Myrberg & Thresher 1974; Cody 1978). Defence of food supplies against heterospecifics has been recorded for a variety of animals, especially fish (e.g. Myrberg & Thresher 1974) and birds (e.g. Lyon et al. 1977; Cody 1978). In some of these studies, territory owners discriminated among intruding heterospecifics and adjusted their level of agonism towards each intruder species based upon factors such as taxonomic distance, dietary overlap and/or perceived threat (Myrberg & Thresher 1974; Lyon et al. 1977).

Northern harriers, *Circus cyaneus*, defend feeding territories against both heterospecific and conspecific intruders (Bildstein & Collopy 1985; Temeles 1986, 1990). Because these territories are maintained only during the winter, defence against heterospecifics presumably ensures adequate food supplies, rather than nesting sites (Temeles 1987). None the less, the mechanisms of food competition between harriers and heterospecifics are unclear. Bildstein & Collopy (1985) noted that some heterospecific intruders (primarily red-tailed hawks, *Buteo jamaicensis*) pirated prey from territorial harriers (also see Bildstein 1987). They suggested that although aggressive defence may prevent heterospecifics from capturing prey within a harrier’s territory, it might also lessen the likelihood of kleptoparasitism, the stealing of already procured food (Brockmann & Barnard 1979). Hence, territorial defence by harriers might reduce both exploitative and interference competition (Bildstein & Collopy 1985).

In this paper, I examine interspecific territoriality of harriers and show that they discriminate among intruding species of raptors. Then, I show that kleptoparasitism has a major influence on the relationships of territorial harriers with intruding raptor species.

METHODS

I studied harriers on agricultural land situated 3 km northeast of Davis, Yolo County, California, U.S.A. (see Temeles 1986, 1987 for detailed descriptions). The flat landscape allowed an unobstructed view of at least 10 km in all directions. I observed 132 h of harrier activities on 24 days from 4 December 1984 to 1 February 1985, and 80 h of harrier activities on 15 days from 30 November 1985 to 22 January 1986.

Harriers were recognized as territorial by their defensive behaviour. I identified individual territory owners by noting plumage characteristics and favourite perch sites (Temeles 1986, 1987). Although this method is less favoured than colour-marking, I did not colour-mark individual territory owners for two reasons. First, they did not respond to baited traps (e.g. bal-chatri), and hence could not be captured using this technique. Second, I did
not use mist-nets because I felt that placement of nets on the study area and subsequent removal of any individuals captured by this method might affect the behavioural processes that I wanted to study (see Gass 1979 for a related discussion). However, I am confident of the accuracy of my method of identification because (1) individual owners varied extensively in plumage characteristics (e.g., missing or damaged feathers; distinctive coloration) and (2) individual owners used the same perches, among many possible, on successive days.

Adult males typically did not defend winter territories at my study area (from 1983–1987, I recorded only one territorial male). Thus, all my data on territorial harriers are from adult females ($N = 6$ in 1984–1985, $N = 5$ in 1985–1986). Because harriers were not permanently marked, I was unable to determine whether I was observing the same individuals in successive years. Hence, sample sizes presented in the Results refer to the numbers of territory owners studied in the two seasons.

I made continuous focal observations of territorial individuals (Altmann 1974) averaging 6.6 h in duration (range: 4–9 h on winter days of 9–10 h daylight; observations were initiated between 0645 and 0800 hours). From these observations, I noted for each territorial individual the date and time of each observation and the sex and age of the bird. I then determined the size and location of its territory, the number of prey-capture attempts and successful captures, the time spent in foraging, perching, eating, or in aggressive interactions, the number and type of intruders entering the bird's territory, and the type of interaction with each intruder. I observed harriers from distances of 20–250 m, using 7 × 35 mm binoculars or a 15–60 × spotting scope when necessary. See Temeles (1986, 1987) for methods concerning identification of territory owners and sex and age classes, measurements of territory areas, determination of capture attempts, capture success and time spent in various activities.

The most frequent heterospecific intruders on harrier territories ($N = 7$ territories) were red-tailed hawks and black-shouldered kites, *Elanus caeruleus*. Less frequent heterospecific intruders were rough-legged hawks, *B. lagopus* and American kestrels, *Falco sparverius*. I considered all four species to be competitors of harriers because: (1) the diet of each species overlaps to some extent with the diet of harriers, (2) individuals of each species hunt and/or capture prey (primarily rodents) on harrier territories, and (3) individuals of each species aggressively interact with harriers.

Once a heterospecific intruder entered a harrier's territory, I assumed that the territorial female had detected the intruder if (1) I could clearly observe her tracking the intruder (as determined from eye, head or body movements), (2) the intruder flew within 5 m of her, or (3) the territorial female flew within 5 m of the intruder. I recorded whether the territorial harrier attempted to evict the intruder aggressively. Aggressive responses always involved flight (e.g., chases of flying intruders or stoops at perched intruders) during which harriers usually gave threat calls (see Bildstein & Colpoy 1985).

Territories differed in both the kinds and numbers of heterospecific intruders (see Temeles 1987). To avoid the problems of unequal sample sizes and pseudoreplication, I used binomial tests of McNemar four-fold frequency tables (Siegel 1956, pp. 66–67) to determine whether the same territory owners responded differently to different species of intruders, and whether these differences in response to intruders were consistent across owners. Other non-parametric statistical procedures follow Siegel (1956).

**RESULTS**

**Responses to Heterospecific Intruders**

Territorial harriers responded aggressively to 29 of 57 (51%) intrusions by red-tailed hawks, 10 of 37 (27%) by rough-legged hawks, none of 116 by black-shouldered kites and none of seven by American kestrels. This difference in aggression towards red-tailed hawks and black-shouldered kites ($\chi^2 = 71$, $df = 1$, $P < 0.0005$) was consistent across seven territory owners for which pairwise comparisons were possible: all seven owners responded aggressively to red-tailed hawks, but none of the seven responded to kites ($P = 0.016$, two-tailed, binomial test of McNemar table).

These differences in frequencies of responses suggest that harriers respond aggressively depending in part on the size of the intruding species. Female harriers (531 g) weigh only half as much as either red-tailed (male = 1028 g, female = 1224 g) or rough-legged hawks (male = 1027 g, female = 1278 g), twice as much as black-shouldered kites (male = 273 g, female = 307 g) and over four times as much as American kestrels (male = 109 g, female = 119 g; weight data from Haverschmidt
1962; Snyder & Wiley 1976). Consequently, I grouped these data into two categories relative to the size of a harrier (i.e. larger heterospecifics and smaller heterospecifics) to assess how the size of the intruder influenced harrier behaviour.

**Interactions with Larger Heterospecifics**

In earlier studies, I determined that territorial harriers encountered two kinds of conspecific intruders: (1) competitors for portions of territories (e.g. other territorial females) and (2) competitors for individual prey items (e.g. non-territorial males and females; Temeles 1986, 1989a, 1990). Because I never observed either red-tailed or rough-legged hawks attempt to displace harriers from their territories, I hypothesized that these two species competed with harriers for prey items rather than for territories.

In those studies, I found that territorial harriers temporarily reduced the intensity of their responses towards competitors for prey items following prey consumption, and often did not respond to them (Temeles 1989a). This reduction in territorial intensity occurred because harriers were restricted from further feeding due to a processing constraint (i.e. the passage rate of food through their crops further down their digestive tracts), and the pay-off from fights over prey items was lowered temporarily once they had eaten (Temeles 1989a, b). Because territorial harriers frequently did not respond to either red-tailed (28 of 57 intrusions; 49%) or rough-legged hawks (27 of 37 intrusions; 73%), one possible explanation for decisions not to respond might be reduced motivation to fight following meals (Temeles 1989a). However, only 7% of the failures to respond to red-tailed hawks (N = 28) and 18% of the failures to respond to rough-legged hawks (N = 27) occurred during periods of food processing. Thus, the responses of territorial harriers to intrusions by larger heterospecifics did not depend on whether harriers had recently consumed prey.

I considered two additional explanations for the response of harriers to larger heterospecific intruders. One was that harriers might respond to these intruders primarily to reduce exploitative competition in the form of hunting and prey capture. If this is the case, territorial harriers should respond aggressively only when larger heterospecifics actively hunt on harrier territories and attempt to capture prey. This prediction was not supported. Harriers responded aggressively on only four of eight occasions when red-tailed hawks attempted to capture prey, but also on 23 of 43 occasions when red-tailed hawks did not attempt to capture prey (P > 0.3, Fisher’s exact test; this analysis excludes cases in which harriers did not respond because of processing constraints, N = 2). Harriers behaved similarly towards rough-legged hawks, responding aggressively during only one of five prey-capture attempts, but also during 7 of 27 occasions when rough-legged hawks did not attempt to capture prey (P > 0.4, Fisher’s exact test; this analysis excludes cases in which harriers did not respond due to processing constraints, N = 5).

Another explanation for the harriers’ aggressive behaviour to larger heterospecifics is that it might reduce interference competition in the form of kleptoparasitism (i.e. they evict larger raptors that could kleptoparasitize them; see the Introduction). I observed three attempts at kleptoparasitism by red-tailed hawks on territorial female harriers (one successful), and one unsuccessful attempt by a rough-legged hawk. If aggression towards larger heterospecifics primarily reduces kleptoparasitism, territorial harriers should respond aggressively only when larger heterospecifics intrude while harriers are hunting. As predicted, harriers attempted to evict 18 of 20 (90%) red-tailed hawks that intruded when the harriers were not hunting, but only 9 of 31 (29%) red-tailed hawks that intruded when the harriers were not hunting (χ² = 18.1, df = 1, P < 0.005). Similarly, harriers attempted to evict all five (100%) rough-legged hawks that intruded when they were hunting, but only 3 of 27 (11%) when they were not hunting (Fisher’s exact test, P < 0.005). Neither analysis included cases in which harriers did not respond because of processing constraints (N = 2 for red-tailed hawks; N = 5 for rough-legged hawks). Hence, the failure of harriers to respond when they were not actively hunting did not result from the need to process food.

**Interactions with Smaller Heterospecifics**

In contrast to their behaviour towards larger heterospecific intruders, territorial female harriers never attempted to evict smaller heterospecific intruders from their territories, even though there was considerable dietary overlap and little prey-size partitioning with these species. At my study area, the primary prey of all these species were rodents (Microtus californicus, Mus domesticus), and
Kestrels and kites were observed to feed on the same sizes of rodents (10-60 g) as harriers (Temeles 1989b and personal observation; also see Warner & Rudd 1975). Moreover, only 7% of failures to respond to kites (8 of 116) and 43% of failures to respond to kestrels (three of seven) occurred during periods of sitting for food processing.

Whereas harriers are kleptoparasitized by larger heterospecific intruders and evict them to reduce this loss by interference, I hypothesized that they in turn might kleptoparasitize smaller heterospecific intruders, rather than evict them. Kleptoparasitism of smaller heterospecific intruders might not only reduce losses from exploitative competition, but might also increase overall energy intake. Certainly kleptoparasitism by territorial harriers was directed only towards smaller heterospecific intruders: harriers attempted kleptoparasitism during 18 of 33 (55%) prey capture attempts by smaller species, but none of 28 prey-capture attempts by larger species (χ² = 21.7, df = 1, P < 0.0005). Specifically, territorial harriers attempted kleptoparasitism during 57% (N = 30) of capture attempts by kites, 33% (N = 3) by kestrels, and 0% by red-tailed (N = 23) and rough-legged hawks (N = 5). This clear difference was consistent across six territory owners for which pairwise comparisons were possible: all six territorial harriers attempted kleptoparasitism during capture attempts by black-shouldered kites, whereas none of the six attempted kleptoparasitism during capture attempts by red-tailed hawks (P = 0.032, two-tailed, binomial test of McNemar table).

Attempts to kleptoparasitize black-shouldered kites, although frequent, were often unsuccessful. Of 11 successful prey captures by kites in which harriers attempted kleptoparasitism, two (18%) were successful. In addition, territorial harriers apparently attempted kleptoparasitism during another six capture sequences in which kites were unsuccessful. In these six cases, harriers pounced on kites that were on the ground in pursuit of prey, and the prey was lost to both birds. Whether the six failed capture attempts were caused by the kites' own behaviour or by the interference from the harriers could not be determined.

Moreover, territorial harriers sometimes did not attempt kleptoparasitism, even though the kites captured prey in full view of the harriers (N = 13 of 30 capture attempts by kites). Studies suggest that a raptor's decision to steal food depends upon its current rate of energy intake: a hungry raptor should kleptoparasitize more often than one that has eaten recently (e.g. Stalmaster & Gessaman 1984; but see Hansen 1986). A female harrier requires about 100 g of food per day for maintenance (Craighead & Craighead 1969), which, based upon measurements at my study area, is roughly equivalent to four mice (Temeles 1989b). Assuming a daylength of 10 h (see Methods), a female harrier would need to capture 0.4 prey/h to satisfy her energy requirements. Consequently, I examined harriers' decisions to kleptoparasitize kites in relation to two categories of energy intake: (1) current energy intake rates greater than or equal to that needed to satisfy energy requirements (0.4 prey/h; duration over which intake rates were assessed, X ± SE = 4.2 ± 0.5 h, N = 7) and (2) current energy intake rates less than that needed to satisfy energy requirements (0.4 prey/h; duration, X ± SE = 4.1 ± 0.6 h, N = 18). When their current rate of energy intake was less than that required for maintenance, harriers attempted kleptoparasitism during 17 of 18 (94%) capture efforts by kites, whereas when their current rate of energy intake was greater than or equal to that required for maintenance, harriers attempted kleptoparasitism in none of seven capture efforts by kites (P < 0.005, Fisher's exact test). In addition, harriers did not attempt to kleptoparasitize kites on five occasions when they were processing food. Thus, for territorial harriers, the decision to kleptoparasitize a smaller intruder apparently depends upon their current rates of energy intake.

Kites and kestrels always left harriers' territories immediately after kleptoparasitism attempts, whether or not these attempts were successful. In addition, kites would leave territories following unsuccessful attempts to displace harriers from the vicinity of their perches. Kites aggressively stooped at harriers in 74 of 133 (56%) encounters. Of the 74 aggressive responses by kites to approaching harriers, 36 occurred while harriers were flying, and hence whether harriers left the vicinity of kites' perches of their own accord or as a result of the kites' behaviour could not be determined. However, the remaining 38 aggressive responses by kites towards harriers occurred while harriers were sitting on the ground near the perches of the kites. Of these 38 responses, 19 (50%) caused the harriers to move away from kites' perches. In the remaining 19 (50%) cases, kites failed to displace sitting harriers and subsequently left the harriers' territories.
In contrast to the behaviour of smaller heterospecifics, excluding kleptoparasitism attempts, larger heterospecific intruders never stooped at harriers (N = 57 interactions between red-tailed hawks and harriers; N = 37 interactions between rough-legged hawks and harriers; differences among kites and red-tailed and rough-legged hawks significant at $\chi^2 = 77.6$, df = 2, $P < 0.005$).

**DISCUSSION**

Territorial female harriers clearly responded differently to different species of intruders. This difference cannot be explained by variation in aggressive behaviour among territorial female harriers, because the results are based upon responses of the same females to all species of intruders (i.e. binomial tests of McNemar tables). Rather, a harrier’s decision to respond aggressively towards an intruder depends on its size relative to that of the harrier, which influences the ability of the harrier to kleptoparasitize or to be kleptoparasitized.

My observation that territorial harriers responded most frequently to larger heterospecifics (e.g. red-tailed and rough-legged hawks) that intruded when the harriers were hunting suggests that they may have been trying to clear the area of potential kleptoparasites. Territorial aggression by harriers against larger heterospecifics thus may function primarily to reduce interference competition, rather than exploitative competition (Bildstein & Collopy 1985).

In contrast, territorial female harriers may reduce losses due to intrusions by smaller heterospecifics (e.g. black-shouldered kites and American kestrels) through kleptoparasitism rather than through aggressive territorial defence. If this is the case, it is reasonable to ask how kleptoparasitism of smaller heterospecifics can be a profitable strategy for defence when it is both partially successful and conditional upon rates of energy intake. Several factors suggest that the benefits of ‘defence by kleptoparasitism’ outweigh the costs, and are greater than the benefits that would be accrued through active defence. Kleptoparasitism of smaller heterospecifics may enable a female harrier to remain on her territory when her hunting success and encounter rate with prey are poor, thus preventing greater losses from intrusions that would result if she either had temporarily abandoned her territory to forage elsewhere or had maintained active defence while continuing to hunt unsuccessfully. In addition, although territorial harriers may experience some losses via exploitation by intruders, prey supplies may be somewhat renewale because of the mobility of harriers’ prey (mammals, birds). Finally, black-shouldered kites aggressively chase individuals of their own and other species (e.g. red-tailed hawks) from the vicinity of their perches (personal observation). As a result, the standing crop (sensu Schoener 1987) of kites within a harrier’s territory is density dependent. Once the density of kites on a harrier’s territory reaches a certain threshold, further addition of kites is prevented by the aggressive behaviour of kites already present. Such ‘territories within territories’ have been observed previously among hummingbird species (Lyon 1976): smaller white-eared hummingbirds, *Hylorchis leucotis*, defended territories within territories of larger blue-throated hummingbirds, *Lampornis clemenciae*.

As noted here, territorial harriers often did not attempt to evict intruders. Schoener (1987) argued that territory owners usually should evict intruders upon detection 100% of the time, with two exceptions: (1) intruders might not be evicted when eviction conflicts with other activities (e.g. foraging, eating, food processing) and (2) intruders might not be evicted when conditions (e.g. open territories) allow owners to monitor fully the activity of intruders. Both exceptions applied to harriers in this study. However, the ability to monitor intruders’ activities apparently is the more important of the two, because it allows territorial harriers to evaluate their potential losses to intruders and then adjust the intensity of their responses accordingly.

Finally, analyses of feeding territoriality (e.g. Hixon et al. 1983; Schoener 1987) have focused primarily on decisions by territory owners to adjust territory size and/or time spent in patrolling for intruders, and for the most part have neglected interactions with different types of intruders. My study indicates that owners of feeding territories can respond differently to different types and species of intruders, according to the threat they present (also see Temeles 1989a, 1990). Hence, for animals defending feeding territories, especially visually open ones, whether to evict intruders and the level of investment in aggression may both be decision variables in addition to territory size and patrol time.
ACKNOWLEDGMENTS

I thank A. Hedrick, K. Bildstein, M. Collopy, L. Drickamer, L. Gass, P. Pietz, T. Schoener, J. Smith and J. Stamps for comments on the manuscript. I also am grateful to the Davis Audubon Society, Heidrick Farms, and Hunt-Wesson Foods, Inc., for granting me access to their lands. My research was supported by Graduate Student and Jastro-Shields Awards and Regents’ and E. C. Anthony Fellowships from the University of California, Davis, and a NATO/NSF Postdoctoral Fellowship (RCD-8854487).

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(Received 7 September 1989; initial acceptance 10 October 1989; final acceptance 27 November 1989; MS. number: A3641)