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Intruder pressure explains more of the variation in territory size than fish abundance for Red-necked Grebes (*Podiceps grisegena*) breeding on small boreal lakes

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In the Red-necked Grebe (*Podiceps grisegena*), breeding pairs use both overt aggression and ritualistic behavior to defend territories for breeding and feeding. Examining the influence of factors determining territory size simultaneously continues to be stressed in studies of territorial systems. The behavior of grebes breeding on small boreal lakes (15–240 ha) was examined in relation to several environmental variables through three stages of the breeding season (pre-nesting, nesting, and post-nesting). Territory size was shown to be inversely related to grebe density and fish abundance during the pre-nesting and nesting stages of the breeding season. In addition, grebe density was more strongly associated with territory size than was fish abundance. The costs and benefits that balance economic decisions for breeding grebes rigorously defending areas are discussed.

1. Introduction

The size of an area that maximizes the difference between the costs and benefits for a breeding pair is referred to as the optimal territory size (Myers *et al*. 1981). Many proposed optimal territory size models vary with respect to the nature of the benefits (*e.g.*, currency), the probability of alternative options (*e.g.*, temporarily non-territorial), and the time scale during which the costs and benefits are measured (*e.g.*, days, months, or seasons) (Myers *et al*. 1981, Hixon 1980, 1982, Schoener 1983).

Food supplies ultimately limit many populations. When food levels are relatively high and uniformly distributed, individuals may acquire enough food to meet their demands without any defense of an area. As food levels decline and become more patchy, individuals may benefit (acquire more food) by displacing competitors. Brown (1964) hypothesized an inverse relationship between food abundance and territory size. Boutin (1990) reviewed the role food plays in shaping life histories, population dynamics, and behavior of terrestrial vertebrates. His literature search revealed that, in 19 of 23 experimental studies, food addition resulted in a decrease in home range size, supporting the food hypothesis.

Territory size is also a function of intruder pressure since increasing food levels attracts more competitors (Hixon 1980, 1982, Schoener 1983). As population densities and intruder pressure increases, territorial species should decrease the size of the area defended in order to maximize the difference between feeding and defending time. This relationship has been observed in several bird species even after the effects of food abundance have been controlled for statistically (Myers *et al*. 1979, Dunk & Cooper 1994).

The Red-necked Grebe (*Podiceps grisegena*) is a species in which both members of the pair actively establish and maintain a territory, construct a nest, incubate the clutch, and care for the young until the time near dispersal. Breeding pairs use both overt and ritualistic aggressive behaviors in defense of territories for breeding and feeding, although they have been reported to defend only breeding territories in areas of high density (Wobus 1964, Stout & Nuechterlein 1999).

Here, we provide field data that quantitatively examine behavioral interactions between adjacent breeding pairs of Red-necked Grebes in Alberta, where they exhibit classical all-purpose territoriality located on small boreal lakes (15–240 ha). Our objective was to quantify and subsequently examine the relationships between intruder pressure, food abundance, and the size of breeding territories.

2. Methods

2.1 Study area and methods

During 1994 and 1995, 34 breeding pairs were observed across 8 small lakes of various sizes in the vicinity of Meanook Biological Research Station, Athabasca County, Alberta, for a total of 352 hr (Table 1). Prior to observation, an effort was made to capture birds with underwater mist nets and subsequently band them with a Canadian Wildlife Service aluminum leg-band and a unique combination of three color-bands. Pairs were observed according to a randomly established rotation schedule; they were observed from shore or boat using binoculars and a spotting scope. Care was taken to remain more than 50 m from focal pairs to minimize disturbance. In 1994, the durations and locations of all behaviors of focal pairs (n = 10) were observed during repeated 1-hr periods of continuous time budgets. In 1995, territories were operationally defined (Maher & Lott 1995) by recording the behavior and position of each member of focal pairs (n = 24) every 5 min through instantaneous scans. Data from 1994 were transcribed to coincide with data from 1995 pairs by extracting locations and behaviors at 5-min intervals. The boundaries of territories were plotted on scaled maps (1:2,500), delineated by minimum convex polygons, and calculated using a digital polar planimeter (Placom Koizumi KP-90).

2.2. Measuring behaviors

Intruder pressure was estimated by counting the number of Red-necked Grebes per hectare present on the lake during behavioral observations. Further estimates were determined from intrusion rates. Overt aggressive behavior involved in the direct displacement of intruders included: (1) threat (movement towards intruder with head ready to fight), (2) high threat (threat with head held high) (Kevan 1970), (3) hunched posture (threat-like posture with head partially back and wings slightly raised) (Cramp & Simmons 1977), (4) underwater pursuit (movement towards surface intruder from underwater), (5) chase (surface movement towards a retreating intruder), (6) pattering (accelerated surface movement while flapping wings), and (7) fights (interaction with strikes, sometimes making physical contact) (Kevan 1970, Garner 1991). Fights with contact were categorized separately due to the potential cost of injury involved when grabbing and holding each other. Ritualized display behavior included visual and vocal displays such as (1) vocal duet displays (vocalize together with head up) (Cramp & Simmons 1977), (2) penguin dances (rise out of the water breast to breast), (3) weed dances (swim together with at least one carrying vegetation), (4) discovery ceremonies (one rises out of the water in front of the other, often following a short separation) (Stout & Nuechterlein 1999), (5) triumph ceremonies (members of a pair conduct exaggerated vocal duet displays and penguin dances immediately following inter-pair conflict) (Stout & Nuechterlein 1999), and (6) vocalizations (Kevan 1970, Garner 1991, Stout & Nuechterlein 1999). Quiet vocalizations were categorized separately and assumed to be inaudible outside the focal territory. Platform behaviors may advertise mating and pair status to adjacent pairs, and included (1) inviting and (2) copulation (Stout & Nuechterlein 1999). During behavioral observations of focal

Table 1. Lake characteristics and number of pairs of Red-necked Grebes present in 1994 and 1995.

Lake name	Location	Area (ha)	Max. Depth (m)	Fish/ No Fish	Pairs[a]		Pairs/ha[a]		# Pairs obs.		# Birds banded	
					1994	1995	1994	1995	1994	1995	1994	1995
Armstrong	54°24’ N, 113°39’ W	239.20	3.42	Fish	40	–	5.98	–	2	0	3	0
Duggan’s	54°13’ N, 113°23’ W	135.07	1.30	No fish	25	–	5.40	–	1	0	1	0
“Grochowski”	54°28’ N, 113°19’ W	64.00	1.45	Fish	14	–	4.57	–	1	0	1	1
Tawatinaw	54°21’ N, 113°28’ W	52.67	4.15	Fish	18	–	2.93	–	2	0	0	0
“Rochester”	54°23’ N, 113°18’ W	17.20	1.82	Fish	8	10	2.15	1.72	1	10	0	3
Gilbert	54°30’ N, 113°10’ W	16.53	1.26	No fish	4	8	4.13	2.07	1	8	0	4
“Turkowski”	54°29’ N, 113°08’ W	15.60	1.53	Fish	6	6	2.60	2.60	1	6	0	3
“Son of Rochester”	54°23’ N, 113°21’ W	14.80	2.23	Fish	6	–	2.47	–	1	0	1	0
All									10	24	6	11

a Peak number at the height of the breeding season.

pairs, we categorized each interaction as either platform, ritualistic, or overt; and plotted its location. We then recorded all the behaviors involved and the total duration of the interaction.

2.3. Estimating resource abundance

Fish were sampled throughout the breeding season. Each territory was sampled at least once monthly (June–August in 1994 and June and July in 1995). Unbaited Gee minnow traps were placed on the bottom throughout each territory for 14–18 hours according to a random stratified design by habitat. Captured fish (fathead minnow, *Pimephales promelas*, and brook stickleback, *Culaea inconstans*) were identified, counted, measured, and released. Twenty-five fish of each species were captured, measured, and weighed to establish a length-weight regression model used to predict live weights from total lengths for biomass estimates. The biomass of each trap was summed, and means were taken for each territory expressed as a catch per unit effort (CPUE).

2.4. Analysis

The relationship between territory size, intruder pressure, and fish abundance was analyzed by nesting stage (pre-nesting, nesting, and post-nesting) using a class of multivariate techniques called ordination (Van Wijngaarden *et al.* 1995). Pre-nesting began when a platform was present and lasted 1–4 days until the first egg was laid. Nesting began when the first egg appeared and continued for 3–4 weeks, while post-nesting began when the first egg hatched and continued for 4–6 weeks. Territory size (ha), four indices of intruder pressure (Red-necked Grebes per hectare (RNG/ha) and number of platform, ritualized, and overt behavioral events), fish abundance (CPUE), lake area (ha), and mean day of observation were used as continuous variables. Along with year (1994 and 1995), the presence or absence of fish was used as a categorical variable since some small lakes at that latitude experience regular winter-kill of their fish fauna. The analyses were organized to examine the amount of variance in the behavioral variables which were ln(x+1) transformed, including territory size, that could be associated with the environmental variables which were relativized proportional to their maximum value. A detrended correspondence analysis (DCA) for each nesting stage indicated gradient lengths appropriate for a redundancy analysis (RDA), a linear direct gradient analysis. Year was removed, or “partitioned,” as a covariable, thus making the final models partial RDAs. A correlation triplot was created from each partial RDA to reveal subsequent relationships. Statistical significance of eigenvalues and behavioral-environmental correlations for all ca-

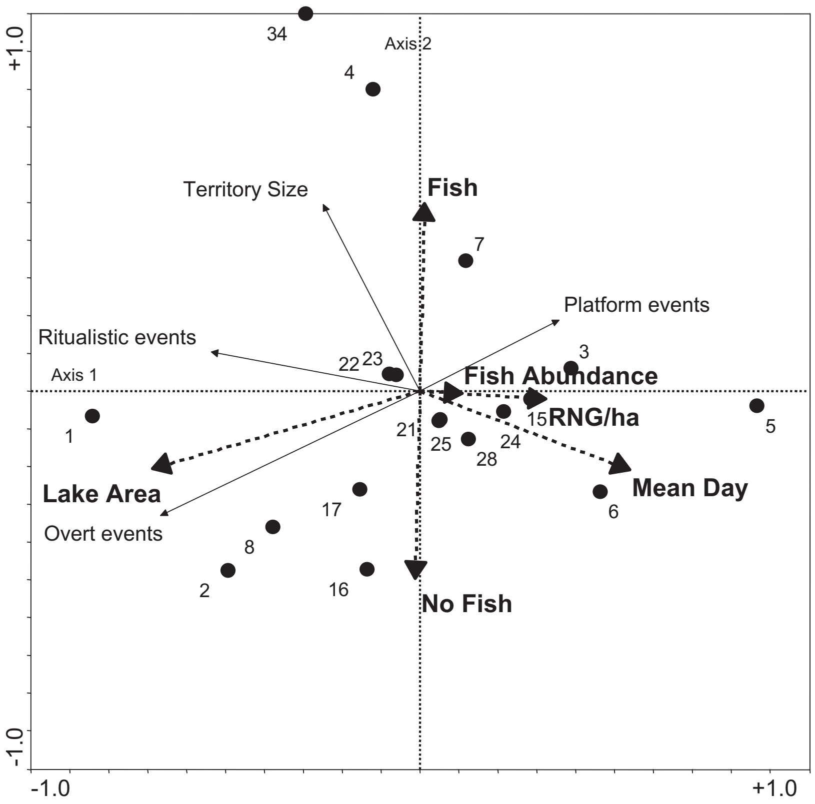

Fig. 1. Results from partial RDA (redundancy analysis) on behavioral variables (thin, solid vectors) and environmental variables (thick, dashed vectors) during pre-nesting. Each pair of grebes is represented by a unique numbered site point.

nonical axes were tested with Monte Carlo tests based on 1,000 permutations. Due to the limitations of a direct gradient analysis (ter Braak 1995), all triplots shown were also checked using principal components analyses (PCA) with environmental variables to indicate that important variables were included in the analyses (Zimmer *et al.* 2000). All ordination procedures were conducted in CANOCO (ter Braak & Smilauer 1998).

3. Results

Partial RDA for both pre-nesting and nesting grebes resulted in models where the environmental variables were significantly associated with the behavioral variables ($P = 0.04$ and $P = 0.001$, respectively) with eigenvalues for the first and second axes being 0.25 and 0.06 for pre-nesting, and 0.24 and 0.07 for nesting (Fig. 1). Direction and strength of vectors indicate a strong positive relationship between lake area and overt aggressive behavioral events, and a weaker negative relationship between grebe densities and fish abundance against territory size and ritualized behavioral events. The territory size vector, and thus the gradient, was perpendicular to that of the lake area and overt aggressive behavioral events gradient, indicating that territory sizes did not change relative to any change in lake area nor overt events. The mean day vector indicates that ritualized behavior, and to a lesser extent territory size, decreased as the season progressed. The platform behavior vector indicates a negative relationship between both overt events and ritualized events. The categorical fish/no fish vectors were closely associated with axis 2 and were, thus, less important early in the season.

The direction and strength of vectors in the RDA triplot for nesting grebes (Fig. 2) indicate that the positive association of lake area and overt behavior continued when the grebes were on eggs. Grebe density and fish abundance became increasingly associated with territory size during the nesting period. The territory size gradient remained perpendicular to that of lake area and overt events.

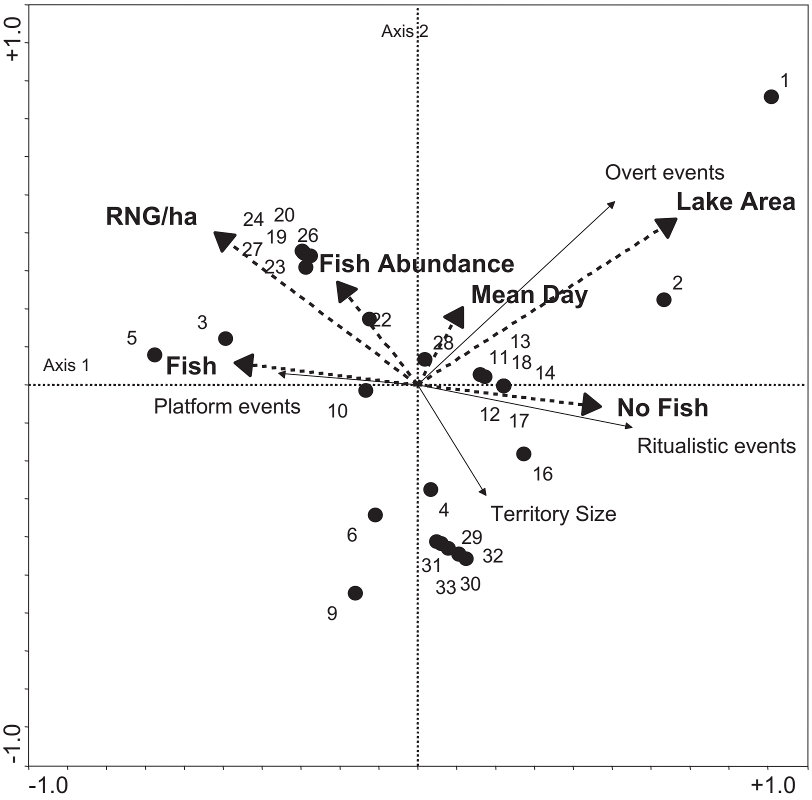

Fig. 2. Results from partial RDA (redundancy analysis) on behavioral variables (thin, solid vectors) and environmental variables (thick, dashed vectors) during nesting. Each pair of grebes is represented by a unique numbered site point.

The mean day vector was shorter and not as negatively related to territory size during nesting as it was during pre-nesting. Yet, platform behavior remained negatively associated with both overt and ritualized behavioral events during nesting. Although they were shorter in the second model, the categorical fish/no fish vectors were more closely associated with axis 1, indicating a stronger relative influence as the season progressed. The environmental variables were not significantly associated with the behavioral variables during post-nesting ($P = 0.72$, eigenvalues axis 1: 0.31 and axis 2: 0.05).

4. Discussion

Our results show that Red-necked Grebe territory size is inversely related to the density of conspecifics and of fish (i.e. food) abundance. This is a common pattern found in many animals (Myers *et al.* 1979, Hixon 1980), and two hypotheses have been proposed to explain such a relationship. The first assumes that animals make economic decisions based on resource availability and defend areas containing sufficient quantities of food (Myers *et al.* 1979, 1981, Norton *et al.* 1982, MacFarland 1986). Although not exclusive from the first, the second hypothesis proposes that animals defend areas as large as possible constrained by the intruder pressure of competitors (Myers *et al.* 1979, Myers *et al.* 1981, Norton *et al.* 1982, MacFarland 1986). Myers *et al.* (1979) stressed the importance of considering prey availability and intruder pressure simultaneously. The RDAs for pre-nesting and nesting also indicate that the vector for grebe density was longer than that for fish abundance which suggests that the number of conspecifics has a larger effect on Red-necked Grebe territory size than the abundance of food. Other studies have shown bird territory size to be explained more by intruder pressure than by food abundance. Myers *et al.* (1979) suggested that Sanderlings (*Caladris alba*) were most influenced by intruder number when defending winter feeding territories. Dunk & Cooper (1994) suggested that Black-shouldered Kites (*Elanus caeruleus*) defend areas as large as possible at any given time constrained by competitor abundances.

The use of space becomes particularly important to birds breeding on discrete wetlands and lakes. The Great Crested Grebe (*Podiceps cristatus*) breeds across Europe and Asia. Although not quantified, Venables & Lack (1934, 1936) suggested that the use of space in the populations they examined was related to available food (small fish), yet more related to intruder pressure. They found high variation in levels of aggression and in the sizes of areas defended. Some pairs were very aggressive, defending areas that they suspected were larger than needed, while others were comparatively passive. The most aggressive pairs were on the smaller bodies of water where they noted intruder pressure to be much more influential on territory size than was food abundance (Venables & Lack 1934, 1936). For the Red-necked Grebes of this study, fish abundance per territory was mainly independent of the size of breeding lake (indicated by the perpendicular vectors in Figs. 1 and 2). However, for the Great Crested Grebe, smaller bodies of water have been characterized by the least amount of food, the largest territories, and the most aggression (Vlug 1983). It has been suggested that pairs have the ability to defend larger areas during low population densities (Simmons 1974, Goc 1986, Ulenaers & Dhondt 1990).

Food abundance may be important for breeding Red-necked Grebes in some areas (Kloskowski 2004). Garner (1991) reported a steady increase in territory size as the season progressed and suggested that it was associated with the demands involved with brooding and feeding young. Parslow-Otus & Elliot (1991) observed a pair of Red-necked Grebes to defend an area of about 2 ha that contained numerous small fish where the competition was intense. During pre-nesting, pairs are establishing territories and initiating nest building. Pre-nesting is also when aggression can become intense enough to delay breeding for many pairs (Kevan 1970). Fjeldså (1973) reported the highest amounts of aggression in Horned Grebes (*Podiceps auritus*) during pre-nesting.

Ritualized display behavior is also important during pre-nesting. The number of ritualistic events increased as territory size increased (Fig. 1). Larger territories require increased movement behavior associated with patrolling borders and interacting with intruders. Thus, territory owners may be able to conserve energy and reduce the risk of escalation during interactions by utilizing ritualistic behaviors that include displays with visual and vocal components.

Once the female begins egg-laying, investments focus on the nest. On larger bodies of water where nests may be relatively aggregated, one member of the pair will often incubate the eggs while the other will swim out to open water away from conspecifics (Klatt *et al.* 2004). In contrast, pairs breeding on the small boreal lakes of this study typically divide the surface area into seemingly equal parts and construct nests in suitable habitat within those areas. Thus, as the number of pairs decease on a given body of water, the remaining pairs expand their territory sizes. For example, the male of a mated pair was found dead on Gilbert Lake in June 1995, possibly killed by a Great Horned Owl (*Bubo virginianus*) (Paszkowski *et al.* 2004). The remaining banded female did not continue incubation of the eggs. However, she did continue to defend an area less than half the size of the original territory for several weeks. Adjacent pairs expanded into her territory until she was eventually displaced by a completely new pair that had appeared on the lake to breed. Adjacent pairs were subsequently pushed back as the new pair squeezed in the available habitat and fought rigorously to establish their territory.

Post-nesting is marked by hatching of the young. Only 13 pairs during this study had at least one egg hatch and cared for their young, which is the best explanation (low sample size) for the environmental variables not being significantly associated with the behavioral variables during that period. Both parents typically participate in brooding the asynchronously hatched young and continue to incubate. Once the family leaves the nest, carrying young on the back, it rarely returns (Stout & Nuechterlein 1999). Pairs may abandon an egg or two, whether addled or otherwise (Wobus 1964, Kevan 1970, De Smet 1987). On larger bodies of water, the parents may take their young out to open water or among other growths of protective vegetation (Kevan 1970, Stout & Nuechterlein 1999, Klatt 2003, Klatt *et al.* 2004). However, the grebes of this study remained on their territories to raise their young. Larger areas relative to food and grebe density may provide increased access to food necessary for feeding young and create a buffer of space to protect them from other pairs (Garner 1991). Young that were several days old have been severely attacked by neighbors as they wandered outside their territory in search of their parents. During this period, grebes with young even become aggressive toward other species (Garner 1991).

A predictable food base is necessary when feeding young. Two of the eight lakes where breeding grebes were observed for this study were fishless. On these lakes, adults and young alike relied solely on macroinvertebrates to fulfill their nutritive requirements. Adults were never seen moving from lake to lake to feed their young, although food flights have been reported elsewhere (Ohanjanian 1989).

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Tunkeilijoiden aiheuttama paine vaikuttaa enemmän reviirikokoon kuin kalan määrä pienillä järvillä pesivällä härkälinnulla (*Podiceps grisegena*).

Pesivät härkälinnut (*Podiceps grisegena*) puolustavat reviiriään sekä ritualistisella että aggressiivisella käyttäytymisellä. Härkälintujen pesimiskäyttäytymistä pienillä boreaalisilla järvillä (15–240 ha) tutkittiin vertaamalla sitä useisiin ympäristöllisiin muuttujiin pesinnän eri vaiheissa. Reviirikoko oli käänteisesti verrannollinen paikallisen härkälintukannan ja kalakantojen kokoon nähden ennen pesintää ja pesinnän aikana. Härkälintutiheydet järvillä vaikuttivat voimakkaammin reviirikokoon kuin kalojen saatavuus.

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