an energetics. Pp. 127–204 *in* Granivorous birds in ecosystems (J. Pinowski and S. C. Kendeigh, Eds.). New York, Cambridge Univ. Press.

KNORR, O. A. 1957. Communal roosting of the Pygmy Nuthatch. Condor 59: 398.

MCNICHOLL, M. K. 1979. Communal roosting of Song Sparrows under snowbank. Can. Field-Natur. 93: 325–326.

NEWTON, I. 1969. Winter fattening in the Bullfinch. Physiol. Zool. 42: 96–107.

PITTS, T. D. 1976. Fall and winter roosting habits of Carolina Chickadees. Wilson Bull. 88: 603–610.

PORTER, W. P. 1969. Thermal radiation in metabolic chambers. Science 166: 115–117.

ROBINSON, D. E., G. S. CAMPBELL, & J. R. KING. 1976. An evaluation of heat exchange in small birds. J. Comp. Physiol. 105: 153–166.

SULKAVA, S. 1969. On small birds spending the night in snow. Aquilo Ser. Zool. 7: 33–37.

TAYLOR, W. K. 1971. A breeding biology of the Verdin, *Auriparus flaviceps* (Sundevall) in Arizona. Amer. Midl. Natur. 85: 289–328.

WALSBERG, G. E. 1986. Thermal consequences of roost-site selection: the relative importance of three modes of heat conservation. Auk 103: 1–7.

———, & J. R. KING. 1978. The heat budget of incubating Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) in Oregon. Physiol. Zool. 51: 92–103.

Received 11 August 1986, accepted 7 February 1987.

The Center-edge Effect: The Result of a War of Attrition Between Territorial Contestants?

LUC-ALAIN GIRALDEAU[1,3] AND RON YDENBERG[2]
[1]*Department of Psychology, University of Toronto, Toronto, Ontario M5S 1A1, Canada, and*
[2]*Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada*

Resident birds often respond more intensely to simulated intrusions at the center than at the edge of their territories [the center-edge (CE) effect; Falls 1982]. Very few hypotheses have been proposed to account for the ecological significance of the effect. Explanations of the CE effect are of two types. First, the intruders are more likely to be closer to residents in the center than at the edge of the territory. It follows that if a resident's response is graded as a function of the distance to the opponent (and not position on the territory), CE effects may be the result of proximity between contestants rather than of the intruder's location on the territory. A second type of explanation argues that the center of a territory has a higher value to a resident than the periphery. We examined the ways territory centers might be more valuable than the periphery and used game theory to generate predictions for each hypothesis. We tested the predictions against data from an exhaustive review of the literature on avian territorial defense.

The intensity of a resident's response to intrusion can vary continuously from mild through intense threat displays, to outright violence. Territorial contests can be analyzed in terms of a war of attrition (Parker 1984). In a war of attrition with no information about opponents (Bishop et al. 1978), the evolutionarily stable strategy is to choose a persistence time based on the ratio V/K, where V is the value of winning and K the rate at which costs can be expended during the contest (Parker 1984). We assumed that the intensity of an individual's response denotes its evaluation of V/K, an assumption supported by Enquist et al. (1985), Ewald and Orians (1983), and Krebs (1982).

The rate at which costs are expended (K) during a contest is set by an animal's resource holding potential (RHP). RHP is not likely to explain the CE effect because, although an individual's RHP can change slowly over time, there is no reason to expect it to change with position on the territory. On the other hand, there are three ways the value of winning (V) can change with the distance from the territory center to the location of the contest. In the *strategic-center hypothesis,* losing possession of the center of a territory more likely leads to loss of the whole territory than does forgoing an equivalent surface at the periphery. The center therefore has a higher strategic value than the periphery. Because all territories have centers, the CE effect should be a characteristic of all territorial defense. In the *central-place foraging hypothesis,* many birds feed their young with food collected on their large territories. If birds defend exclusive access to food resources located around a central nest, then the value of winning exclusive access declines with distance from the territory center. This is because the rate of food delivery to the nest declines

[3] Present address: Department of Biology, Concordia University, 1455 ouest, Boulevard de Maisonneuve, Montréal, Québec H3G 1M8, Canada.

TABLE 1. Presence or absence of differential response to intrusions at the territory center and periphery in 24 species. Information was obtained by observation (O), playback (P), or stuffed or live model (M). Territories were classified as central-place foraging (CPF) or central nonfood resource (CR).

Family	Species	Method	CPF	CR	Source
Cases with center-edge effect					
Corvidae	*Corvus corone*	M	Yes	Nest	Spray 1978
	Pica pica	M	Yes	Nest	Baeyens 1981
Fringillidae	*Spizella pusilla*	P	Yes	Nest	Goldman 1973
	Zonotrichia albicollis	P	Yes	Nest	Falls and Brooks 1975, Melemis and Falls 1982
Laridae	*Larus atricilla*	O	No	Nest	Burger and Beer 1975
Haematopolidae	*Haematopus ostralegus*	O, M	Yes	Nest	Vines 1979
Mimidae	*Dumetella carolinensis*	P	Yes	Nest	Harcus 1973
Paridae	*Parus major*	P	Yes	Nest	Dhondt 1966, Falls et al. 1982
Parulidae	*Dendroica discolor*	O	Yes	Nest	Nolan 1978
	Setophaga ruticilla	P	Yes	Nest	Ickes and Ficken 1970
Cases with no center-edge effect					
Icteridae	*Agelaius icterocephalus*	P	No	Nest	Wiley and Wiley 1980
Motacillidae	*Motacilla alba*	O	No	No	Davies and Houston 1981
Laridae	*Larus ridibundus*	O	No	Nest	Patterson 1965
Scolopacidae	*Numenius arquata*	O	No	No	Ens and Zwarts 1980
Tetraonidae	*Centrocercus urophasianus*	O	No	No	Wiley 1973
	Lyrurus tetrix tetrix	O	No	No	Kruijt and Hogan 1967
Trochilidae	*Amazilia tzacatl*	O	No	No	Boyden 1978
	Atthis heloisa	O	No	No	Lyon 1976
	Colibri thalassinus	O	No	No	Lyon 1976
	Eugenes fulgens	O	No	No	Lyon 1976
	Hylocharis leucotis	O	No	No	Lyon 1976
	Lampornis clemenciae	O	No	No	Lyon 1976
	L. amethystinus	O	No	No	Lyon 1976
	Selasphorus rufus	O	No	No	Paton and Carpenter 1984

as distance between the food and the nest increases (Ydenberg et al. 1986). If the CE effect is the result of central-place foraging, then the effect should be present only in territories that are used for central-place foraging and contain the central place. The intensity of the resident's response to intruders should decrease gradually with distance from the central place. In the *central-resource hypothesis*, the center of the territory may contain a discrete resource (nest, young, refuge) that makes it more valuable than the rest of the territory. The CE effect should occur only when the centers of territories contain such a resource.

We collected results from 21 studies dealing with 24 species in 12 families (Table 1). Evidence for a CE effect was found in 42% (10/24) of the species. Because the strategic-center hypothesis predicts CE effects for all territories, it cannot account for the distribution of CE effects. The 9 species with CE effects used their territories for central-place foraging, while the 14 species without CE effects did not. Of 15 species with a non-central-place foraging territory, only 1 (*Larus atricilla*; Burger and Beer 1975) showed a CE effect. In *L. ridibundus*, however, when proximity between contestants was kept constant the CE effects disappeared (Patterson 1965). Only 2 of the 10 studies that reported CE effects controlled for contestant proximity (Ickes and Ficken 1970, Vines 1979), suggesting that the number of instances of CE effects reported in the literature may be overestimated. The prediction of the central-place foraging hypothesis therefore is consistent with the distribution of CE effects.

Unfortunately, there are important problems with the data set that warrant caution in the interpretation of the results. Of the 14 species reported to show no CE effect, only 1 was studied experimentally. The data for the other 13 species came from observational studies in which the author(s) stated that the intruders were invariably chased upon detection. We assumed this meant that owners used a maximum-intensity behavior (chase) in response to all intrusions irrespective of their location. Because chases are the most conspicuous form of territory defense, however, the lack of CE effects may not be the result of observational bias. More quantitative evidence from experimental studies is required.

Although our results match the predictions of the central-place foraging hypothesis, they are also consistent with the central-resource hypothesis. All 12 species on territories without a central resource lacked CE effects, while 10 of the 12 species on territories with central resources showed CE effects. Thus, although we can reject the strategic-center hypothesis,

we cannot distinguish between the central-place foraging and the central-resource hypotheses because territories used for central-place foraging will often be territories with central resources.

One could distinguish between the central-place foraging and central-resource hypotheses by investigating how defense intensity changed with distance from the center of the territory. Because the response intensity is based on an individual's V/K and because K is unlikely to change with distance, only changes in V are likely to influence the response. The central-place foraging hypothesis correctly predicts a decelerating decline in V with distance from the central place, as observed by Vines (1979) and Melemis and Falls (1982). Unfortunately, there are no equivalent models for predicting the change in defense intensity with distance to a central resource. Arguments can be made for either gradual or abrupt decreases in V with distance. Without better predictions from the central-resource hypothesis we must conclude that the observations are consistent with the predictions of the central-place foraging hypothesis.

We could distinguish between the competing hypotheses by examining the territorial defense of central-place foragers that do not forage on their territories. Only the central-place foraging hypothesis predicts the absence of CE effects in all cases. We have found only three avian studies of this type (Table 1). Two of the three cases, including the most detailed analysis (Wiley and Wiley 1980), failed to find a CE effect. The case in which an effect was reported fails to control for proximity (Burger and Beer 1975). These results suggest that the central-resource hypothesis is incorrect. Territories that are not used to collect food by central-place foragers do not show CE effects. Admittedly, the nonforaging territories of the three species of central-place foragers used in this analysis are considerably smaller than the territories on which CE effects usually are described. It is not clear, however, how territory size can affect the existence and observation of CE effects. More experimental studies are required before one or both of the hypotheses can be rejected. The studies should focus on the defense of large territories that are not used for central-place foraging.

We conclude that the center-edge effect is not a universal property of avian territorial defense. The results of our analysis suggest that the center-edge effect arises because of a systematic change in the fitness value of exclusive use of a territory parcel as a function of distance from the central place. In the case of central-place foraging species, we understand how the fitness value changes with distance. A game-theoretical framework provides a consistent explanation for the occurrence of center-edge effects. A similar game-theoretical interpretation of neighbor-stranger discriminations also proved useful in understanding the underlying ecology of aggressive behavior (Ydenberg et al. in press).

We thank J. Bruce Falls for numerous suggestions (including the strategic-center hypothesis) and Pete McGregor for commenting on an earlier version of the manuscript. L.-A. Giraldeau was supported from a NSERC Postdoctoral Fellowship and a NSERC operating grant to Jerry Hogan. R. Ydenberg was supported by a NSERC University Research Fellowship and Operating Grant.

Literature Cited

Baeyens, G. 1981. The role of the sexes in territory defense in the Magpie (*Pica pica*). Ardea 69: 69–82.

Bishop, D. T., C. Cannings, & J. Maynard Smith. 1978. The war of attrition with random rewards. J. Theor. Biol. 74: 377–388.

Boyden, T. C. 1978. Territorial defense against hummingbirds and insects by tropical hummingbirds. Condor 80: 216–221.

Burger, J., & C. G. Beer. 1975. Territoriality in the Laughing Gull (*L. atricilla*). Behaviour 55: 301–320.

Davies, N. B., & A. I. Houston. 1981. Owners and satellites: the economics of territory defence in the Pied Wagtail *Motacilla alba*. J. Anim. Ecol. 50: 157–180.

Dhondt, A. A. 1966. A method to establish the boundaries of bird territories. Gerfaut 56: 404–408.

Enquist, M., E. Plane, & J. Roed. 1985. Aggressive communication in fulmars (*Fulmarus glacialis*) competing for food. Anim. Behav. 33: 1007–1020.

Ens, B., & L. Zwarts. 1980. Territoriaal gedrag bij wulpen buiten het broedgebeid. Watervogels 5: 155–169.

Ewald, P. W., & G. H. Orians. 1983. Effects of resource depression on use of inexpensive and escalated aggressive behavior: experimental tests using Anna's Hummingbird. Behav. Ecol. Sociobiol. 12: 95–101.

Falls, J. B. 1982. Individual recognition by sounds in birds. Acous. Comm. Birds 2: 237–278.

———, & R. J. Brooks. 1975. Individual recognition by song in White-throated Sparrows. II. Effects of location. Can. J. Zool. 53: 1412–1420.

———, J. R. Krebs, & P. K. McGregor. 1982. Song matching in the Great Tit (*Parus major*): the effect of similarity and familiarity. Anim. Behav. 30: 997–1009.

Goldman, P. 1973. Song recognition by Field Sparrows. Auk 90: 106–113.

Harcus, J. L. 1973. Song studies in the breeding biology of the Catbird *Dumetella carolinensis* (Aves: Mimidae). Ph.D. dissertation, Toronto, Ontario, Univ. Toronto.

Ickes, R. A., & M. S. Ficken. 1970. An investigation of territorial behavior in the American Redstart utilizing recorded song. Wilson Bull. 82: 167–176.

KREBS, J. R. 1982. Territorial defence in the Great Tit (*Parus major*): do residents always win? Behav. Ecol. Sociobiol. 11: 185–194.

KRUIJT, J. P., & J. A. HOGAN. 1967. Social behavior on the lek in Black Grouse *Lyrurus tetrix tetrix* (L.). Ardea 55: 203–240.

LYON, D. L. 1976. A montane hummingbird territorial system in Oaxaca, Mexico. Wilson Bull. 88: 280–299.

MELEMIS, S. M., & J. B. FALLS. 1982. The defense function: a measure of territorial behavior. Can. J. Zool. 60: 495–501.

NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. Ornithol. Monogr. No. 26.

PARKER, G. A. 1984. Evolutionarily stable strategies. Pp. 30–61 *in* Behavioural ecology: an evolutionary approach (J. R. Krebs and N. B. Davies, Eds.). Sunderland, Massachusetts, Sinauer Assoc.

PATON, D. C., & F. L. CARPENTER. 1984. Peripheral foraging by territorial Rufous Hummingbirds: defense by exploitation. Ecology 65: 1808–1819.

PATTERSON, I. J. 1965. Timing and spacing of broods in the Black-headed Gull *Larus ridibundus*. Ibis 107: 433–459.

SPRAY, C. J. 1978. Territorial behaviour of the Carion Crow *Corvus corone* L. in relation to food supply: an experimental study. Ph.D. dissertation, Aberdeen, Scotland, Univ. Aberdeen.

VINES, G. 1979. Spatial distribution of territorial aggressiveness in Oystercatchers, *Haematopus ostralegus*. Anim. Behav. 27: 300–308.

WILEY, R. H. 1973. Territoriality and non-random mating in Sage Grouse, *Centrocercus urophasianus*. Anim. Behav. Monogr. 6: 87–169.

———, & M. S. WILEY. 1980. Territorial behaviour of a blackbird: mechanisms of site-dependent dominance. Behaviour 73: 130–154.

YDENBERG, R. C., L.-A. GIRALDEAU, & J. B. FALLS. In press. Neighbours, strangers, and the asymmetric war of attrition. Anim. Behav.

———, ———, & D. L. KRAMER. 1986. Interference competition, foraging asymmetries and the social relationships of central place foragers. Theoret. Pop. Biol. 30: 26–44.

Received 28 August 1986, accepted 7 February 1987.

On the Extent and Source of Instability in Avian Nomenclature, as Exemplified by North American Birds

STORRS L. OLSON
Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560 USA

Among the proposals considered at meetings of the Standing Committee on Ornithological Nomenclature (SCON) held during the XIX International Ornithological Congress in Ottawa, June 1986, was one to create a separate set of rules of nomenclature for ornithology. The need for this originated in part from the debatable viewpoint that birds are "very well known globally, and most problems in their nomenclature have been solved with a resulting high level of stability" as opposed to "imperfectly known" invertebrate groups whose "nomenclature is still in a state of flux . . ." (W. J. Bock, SCON chairman, memorandum of 8 May 1986).

Although SCON stopped short of departing from the rest of zoology and decided it should work within the framework of the International Code of Zoological Nomenclature, the committee agreed at the outset to embrace a "Principle of Established Usage," because the fundamental principle of the International Code, the Law of Priority, was perceived as a threat to the stability of avian nomenclature.

In the first half of this century, most systematic ornithologists, at least in North America, were content to follow the law of priority, in conformance with the Code of Nomenclature as set forth by the A.O.U. (1908: x): "the whole course of scientific nomenclature has shown that the *law of priority—lex prioritatis*—is the one great underlying principle." Dissenting viewpoints had been expressed previously, and attempts were made to set some sort of a statute of limitation in modification of the law of priority, or to adopt the nomenclature that had been used by the most previous authors, the so-called *auctorum plurimorum* principle. These efforts to abrogate the law of priority were rejected unequivocally by the A.O.U. Code (1908: xlvii): "The 'statute of limitation' principle is akin to the *auctorum plurimorum* rule; both are Utopian, and both radically set at defiance the *lex prioritatis*."

Later, however, a reaction again arose to the strict application of the law of priority, and further attempts were made to modify it (reviewed by Mayr et al. 1953: 215–220). This eventually led to the notorious Article 23b (the "fifty year rule") of the International Code of Zoological Nomenclature (ICZN 1964), a rule so contentious and unsatisfactory that it was changed in the next edition of the Code, although it was hardly improved. At present, all cases involving "unused" senior synonyms are supposed to be referred to the ICZN while "existing usage" is maintained. "Estab-