Ecological correlates of territory and home range size in North American dabbling ducks

THOMAS D. NUDDS AND C. DAVISON ANKNEY

Socio-ecology's main focus is upon correlations between social organization and species' differences in ecology (Crook 1970). Among waterfowl biologists there has been considerable disagreement concerning the existence and function of territories (see Ryder 1975, Mineau & Cooke 1979, Owen & Wells 1979, for reviews of the literature and the nature of the problem for geese). McKinney (1965) reviewed the literature about ducks. For example, Hochbaum (1944) thought that intraspecific aggression by ducks (frequently referred to as 'spacing behaviour') 'fit' the definition of classical avian territoriality, but Sowls (1955) proposed that ducks had broadly overlapping home-ranges and did not exhibit territoriality. A main problem has been the use of the word 'territory' where a defended area was not obvious (Dzubin 1955; McKinney 1965).

One interpretation of intraspecific aggression is that it functions in mate attraction and pair-bonding. Broad comparisons of species' natural histories with plumage and behavioural characteristics in different environments support that view (e.g., Siegfried 1976, for oxyurids). Additionally, intraspecific aggression might ensure undisturbed feeding, copulation or incubation for breeding pairs. Broad comparisons support that hypothesis also (see Titman & Seymour 1980 for review).

As a third alternative, McKinney (1965, 1973) hypothesized that the degree of intraspecific aggressive behaviour of ducks would be a positive function of the degree of defendability (Brown 1964) of their respective food resources. McKinney's comparisons support that view. Northern Shoveler *Anas clypeata*, for example, which feed primarily on abundant cladoceran arthropods or on planorbid snails (Swanson *et al.* 1979), show frequent male intolerance of other males and the pair-bond is long-lasting. Shovelers approach the case of classical avian territoriality; their food resources are relatively easy to defend and the areas frequented by pairs are small. In contrast, Pintail *A. acuta* are more promiscuous and males are more tolerant of one another. The food resources they use are 'patchy', being locally abundant but variable in time and space (Krapu 1974), and economical defence of such a resource is less likely. Mallard *A. platyrhynchos* appear to occupy an intermediate position on this continuum of duck social organization. Derrickson (1978, 1979), Dwyer *et al.* (1979), Gilmer *et al.* (1974), and McHenry (1971) reiterated the importance of resource 'patchiness' in understanding differences in the mobility and social behaviour of ducks.

Any general theory to account for the diversity of social organizations of ducks must take into account both resource 'patchiness' and the positive relationship between body size and territory size in birds (Schoener 1968). Generally, larger organisms require more energy and need larger foraging areas because they feed optimally on large prey which are relatively scarce. Thus, interspecific variation in sizes of areas used by breeding ducks may be due to (1) differences in body size and (2) the spatial and temporal variability of resources. For example, Mallard and similar-sized Black Duck *A. rubripes* are considered ecological equivalents by Bellrose (1976). Territories of Black Duck conformed to the configurations of habitat in an Atlantic coast marsh (Seymour & Titman 1978). Males defended entire ponds, the largest of which was 4·0 ha, and all nests were closer to defended ponds than to any other water body. Neighbouring pairs avoided each other's areas after boundaries were established. Mallard in the prairie-pothole region, in contrast, occupied large overlapping areas, and loafing and feeding sites were considerable distances from the nest (Dwyer *et al.* 1979). Despite the similarity in body size, Black Duck conform better to the classical definition of territorial behaviour than do Mallard.

At a gross level of comparison, large marshes are less heterogeneous environments than pothole habitats. Large marshes may 'drawdown' during drought periods but seldom disappear completely, so temporal fluctuations in resources may be damped. Potholes are extremely variable and seasonal and annual variation in pothole abundance is large (Smith 1971;

Wildfowl 33 (1982):58–62

Stoudt 1971). Large marshes are structurally an interspersion of water and aquatic vegetation. Pothole habitats contain patches of water and aquatic vegetation dispersed among upland habitats.

Table 1 is a compilation of quantitative data from the literature on territory and home-range sizes of *Anas* spp., classified according to the type of breeding habitat. Body-weight are data from Bellrose (1976). The data suggest (Figure 1) a component of territory/home-range size variance that is related to body-size ($r = 0{\cdot}44$, $P < 0{\cdot}06$, all data; $r = 0{\cdot}60$, $P < 0{\cdot}01$, 'pothole' data only). In addition there is a component of intraspecific variation that suggests that larger areas are, in general, necessary to produce adequate resources for breeding in 'patchy' environments. Areas are larger in pothole than marsh habitats ($t = 2{\cdot}47$, $P < 0{\cdot}05$).

The pattern is most striking, considering the variability inherent in published data such as differences in the time when territory or home-range was measured, in definition of territory and home-range, and in population size (which may affect territory/home-range size).

The pattern of intraspecific variation in territory/home-range size both clarifies and reinforces McKinney's hypothesis that the diversity of duck social systems is related to the characteristics of resources in breeding habitats. We explicitly account for the contributions that variability of body-size and of food resources separately make to variance in the size of areas used by breeding dabbling ducks.

The hypothesis that intraspecific variation in territory/home-range size is related to resource dispersion is not new. Trautman (1949, cited by Sowls 1955) wondered if '. . . changing water levels or other factors make territory hunting more difficult'. Dzubin (1955) realized that geographic variation in territorial behaviour existed and might be attributable to variation in the type of breeding habitats occupied, and that territory should not be rigidly defined. Smith (1971) observed that Mallard and Pintail territorial behaviour was considerably different in eastern and western regions of the prairies and suggested that 'breeding habitat requirements of the eastern populations may produce a different spatial distribution than that of western populations'.

Although differences in the social organization displayed by ducks are apparent, they may grade into one another as dictated by the costs of defending resources in different environments, and different body sizes and/or diets. Wiens (1976) proposed a continuum of social organizations from rigid territoriality where resources are spatially and temporally predictable and the cost of resource defence is low, to flocks and nomadism where resources are unpredictable and the expense of defence is high. Among the Anatinae reviewed here loose territoriality, home-ranges, and coloniality represent

Table 1. Body weights and territory or home-range sizes of ducks in pothole and marsh habitats.

Species	Body weight (kg)	Home range size (ha)	Habitat	Source
A. platyrhynchos	1·18	283*	pothole	Dzubin 1955
		468	pothole	Dwyer *et al.* 1979
		203†	pothole	Titman 1973
		230	pothole	Gilmer *et al.* 1975
A. rubripes	1·18	4	marsh	Seymour & Titman 1978
A. strepera	0·90	28	marsh	Gates 1962
A. acuta	0·95	486	pothole	Drewien 1968
		509	pothole	Derrickson 1978
A. crecca	0·32	243‡	pothole	Drewien 1967
A. discors	0·42	8*	marsh	Gates 1962
		103	pothole	Dzubin 1955
		65	pothole	Drewien 1968
		36	pothole	Evans & Black 1956
		7	pothole	McHenry 1971
		0·7	pothole	Stewart & Titman 1980
A. cyanoptera	0·34	8*	marsh	Gates 1962
A. clypeata	0·66	8*	marsh	Gates 1962
		3	marsh	Seymour 1974
		20	pothole	Poston 1974

* Maximum (marsh) or minimum estimates (pothole); † Calculated; ‡ Based on a single pair only.

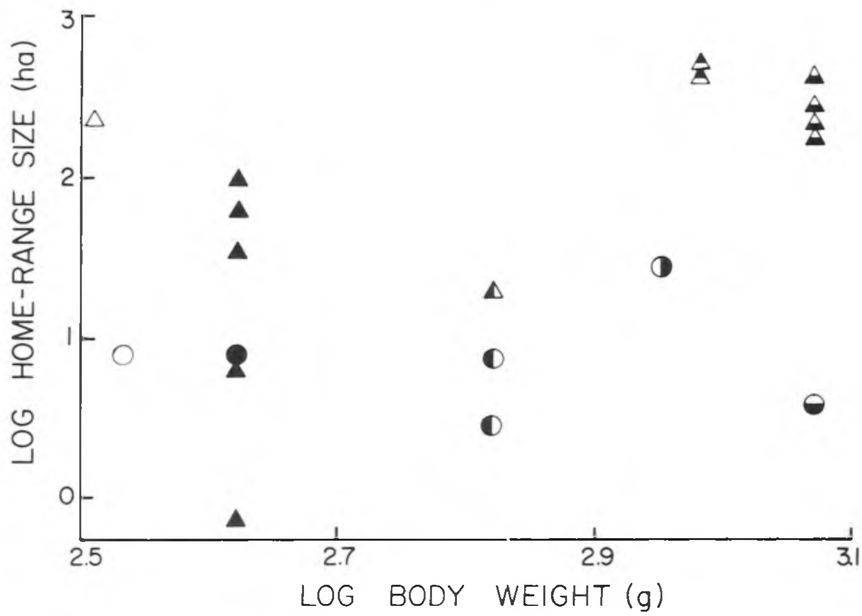

Figure 1. The relationship between body weight and home-range size for some North American Anatinae. Triangles are pothole data, circles are marsh data. Species are coded as follows: *Anas crecca*, open triangle; *A. cyanoptera*, open circle; *A. discors*, closed; *A. clypeata*, left-shaded; *A. strepera*, right-shaded, *A. acuta*, upper-shaded; *A. platyrhynchos* (and *A. rubripes*), lower-shaded.

intermediate types of organization adapted to increasingly variable or unpredictable resources. Additionally, Dzubin (1955) observed that in the arid and unpredictable short-grass prairie region, ducks nest in colonies, and Frith (1959) described the nomadic movements of waterfowl in the unpredictable habitats of inland New South Wales. On the other hand, Ball *et al.* (1978) speculated that the stability of river habitats promoted the evolution of rigid territoriality in African Black Duck *A. sparsa*.

We may speculate about several additional points concerning Figure 1. First, if the abscissa were transformed to convey the size of the food ducks eat, Shoveler would occupy the extreme left-hand position and the fit of the data would be improved. Apart from the Shoveler, there is a regular increase in the number of lamellae per cm of bill (i.e., finer spacing) and decrease in bill size with decreasing body size within the *Anas* (Nudds & Kaminski, unpub.). This suggests that the underlying selective force favouring larger areas being used by ducks with larger bodies is the lesser availability of food of the preferred size for the larger birds.

Second, the lowest data points for Blue-winged Teal *A. discors*, reported by McHenry (1971) and Stewart & Titman (1980), were both estimates for the pothole region near Minnedosa, Manitoba. McHenry said that his estimate of home-range size was less than that reported by others because, in his region, pothole density was high. We suggest that smaller areas are affordable by Blue-winged Teal in habitats comprising closely-spaced potholes which are more marsh-like with respect to resource dispersion.

Third, Black Duck in Atlantic coast marshes occupy areas in the same size-range as do Shoveler, a species about half their weight, in other marsh habitats. Perhaps an increase in the number of potential competitors may reduce resource levels and force the use of larger areas (Yeaton & Cody 1974). Black Duck in Atlantic coast marshes of low competitor diversity may thus benefit, this being reflected in the small areas they occupy there. Other variation in Figure 1 might be accounted for if we knew of the number of coexisting *Anas* species at each study site.

We have necessarily been less concerned with the historical semantic arguments about what constitutes territories or home-ranges, have sacrificed some detail in favour of discovering broadly applicable principles, and have concerned ourselves with the biological significance of observed patterns of variation in the size of areas used by pairs of breeding ducks. This review goes some distance towards reconciling differences of opinion regarding 'territorial' behaviour and its function in ducks. Because duck populations appear to be in evolutionary equilibria with resource levels (Nudds 1980), we hypothesize that interference competition has evolved a diversity of forms depending on the heterogeneity of resources in space and ecological time. In the future, consistent, operational definitions of territory and home-range, improved diet analysis, radiotelemetric techniques, and quantification of temporal and spatial resource variability for several species among different habitats will enable us to assess the various hypotheses regarding the function of intraspecific aggression by ducks.

Acknowledgements

We thank K. F. Abraham, R. O. Bailey, R. W. Cole, F. McKinney, P. Mickelson, J. S. Millar, T. W. Schoener, and R. D. Titman for critical reviews of a draft of the manuscript. This work was supported by the Natural Sciences and Engineering Research Council of Canada, Canadian Wildlife Service, US Fish and Wildlife Service, University of Western Ontario Foundation of New York, Department of Indian and Northern Affairs, and the Canadian National Sportsmen's Fund. The senior author was supported by Natural Sciences and Engineering Research Council of Canada Postgraduate, and Ontario Graduate, Scholarships.

Summary

A review of published, quantitative data suggested that the sizes of areas used by breeding *Anas* spp. is related to both body-size and resource dispersion. McKinney's hypothesis did not distinguish the separate contributions of each of those factors. The variability in social systems among dabbling ducks is correlated with the spatial and temporal variability of breeding habitats; social systems can be arranged along a continuum with 'rigid' territoriality common in stable habitats, but 'loose' territoriality and home-ranges prevailing in variable habitats.

References

Ball, I. J., Frost, P. G. H., Siegfried, W. R. & McKinney, F. 1978. Territories and local movements of African Black Ducks. *Wildfowl* 29: 61–9.

Bellrose, F. C. 1976. *Ducks, geese, and swans of North America.* Harrisburg, Pa.: Stackpole Co.

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.* 76: 160–9.

Derrickson, S. R. 1978. The mobility of breeding Pintails. *Auk* 95: 104–14.

Derrickson, S. R. 1979. Social interactions and spacing behaviour in breeding dabbling ducks (Abstract). Pp. 45 in T. A. Bookhout (ed.). *Waterfowl and wetlands—an integrated review.* LaCrosse, Wis.: LaCrosse Printing Co.

Crook, J. H. 1970. Social organization and the environment: aspects of contemporary social ethology. *Anim. Behav.* 18: 197–209.

Drewien, R. C. 1968. Ecological relationships of breeding Blue-winged Teal to prairie potholes. M.Sc. Thesis, S. Dakota State Univ.

Dzubin, A. 1955. Some evidences of home range in waterfowl. *Trans. N. Amer. Wildl. Conf.* 20: 278–98.

Dwyer, T. J., Krapu, G. L. & Janke, D. M. 1979. Use of prairie pothole habitat by breeding Mallards. *J. Wildl. Manage.* 43: 526–31.

Evans, D. C. & Black, K. E. 1956. Duck production studies on the prairie potholes of South Dakota. *U.S. Fish and Wildl. Serv. Spec. Sci. Rept.* (*Wildlife*) No. 32.

Frith, H. J. 1959. The ecology of wild ducks in inland New South Wales. II. Movements. *C.S.I.R.O. Wildl. Res.* 4: 108–30.

Gates, J. M. 1962. Breeding biology of the Gadwall in northern Utah. *Wilson Bull.* 74: 43–67.

Gilmer, D. S., Ball, I. J., Cowardin, L. M., Reichmann, J. H. & Tester, J. R. 1975. Habitat use and home range of Mallards breeding in Minnesota. *J. Wildl. Manage.* 39: 781–9.

Hochbaum, H. A. 1944. *The Canvasback on a prairie marsh.* Washington, D. C.: Amer. Wildl. Inst.

Krapu, G. L. 1974. Foods of breeding pintails in North Dakota. *J. Wildl. Manage.* 38: 408–17.

McHenry, M. G. 1971. Breeding and post-breeding movements of Blue-winged Teal (*Anas discors*) in southwestern Manitoba. Ph.D. Thesis, Univ. of Oklahoma.

McKinney, F. 1965. Spacing and chasing in breeding ducks. *Wildfowl* 16: 92–106.

McKinney, F. 1973. Ecoethological aspects of reproduction. Pp. 6–21 in D. S. Farner (ed.). *Breeding biology of birds.* Washington, D.C.: National Acad. Sci.

Mineau, P. & Cooke, F. 1979. Territoriality in Snow Geese or the protection of parenthood—Ryder's and Inglis's hypotheses re-assessed. *Wildfowl* 30: 16–19.

Nudds, T. D. 1980. Resource variability, competition and the structure of waterfowl communities. Ph.D. Thesis, Univ. of Western Ontario.

Owen, M., & Wells, R. 1979. Territorial behaviour in breeding geese—a re-examination of Ryder's hypothesis. *Wildfowl* 30: 20–26.

Poston, H. J. 1974. Home range and breeding biology of the Shoveler. *Can. Wildl. Ser. Rept. Ser.* 25.

Ryder, J. P. 1975. The significance of territory size in colonial nesting geese—an hypothesis. *Wildfowl* 26: 114–16.

Schoener, T. W. 1968. Sizes of feeding territories among birds. *Ecology* 49: 123–41.

Seymour, N. R. 1974. Territorial behaviour of wild Shovelers at Delta, Manitoba. *Wildfowl* 25: 49–55.

Seymour, N. R. & Titman, R. D. 1978. Changes in activity patterns, agonistic behaviour, and territoriality of Black Ducks (*Anas rubripes*) during the breeding season in a Nova Scotia tidal marsh. *Can. J. Zool.* 56: 1773–85.

Siegfried, W. R. 1976. Social organization in Ruddy and Maccoa Ducks. *Auk* 93: 560–70.

Smith, A. G. 1971. Ecological factors affecting waterfowl production in the Alberta parklands. *U.S. Fish and Wildl. Serv. Resour. Publ.* 98.

Sowls, L. K. 1955. *Prairie ducks.* Washington, D.C.: Wildl. Manage. Inst.

Stewart, G. R. & Titman, R. D. 1980. Territorial behaviour by prairie pothole Blue-winged Teal. *Can. J. Zool.* 58: 639–49.

Stoudt, J. H. 1971. Ecological factors affecting waterfowl production in the Saskatchewan parklands. *U.S. Fish and Wildl. Serv. Resour. Publ.* 99.

Swanson, G. A., Krapu, G. L. & Serie, J. R. 1979. Foods of laying female dabbling ducks on the breeding grounds. Pp. 47–58 in T. A. Bookhout (ed.). *Waterfowl and wetlands—an integrated review.* LaCross, Wis.: LaCrosse Printing Co.

Titman, R. D. 1973. The role of the pursuit flight in the breeding biology of the Mallard. Ph.D. Thesis, University of New Brunswick.

Titman, R. D. & Seymour, N. R. 1980. A comparison of pursuit flights by six North American ducks of the genus *Anas. Wildfowl* 32: 11–18.

Wiens, J. A. 1976. Population responses to patchy environments. *Ann. Rev. Ecol. Syst.* 7: 81–120.

Thomas D. Nudds, Department of Zoology, University of Western Ontario, London, Ontario N6A 5B7, Canada. Present address: Department of Zoology, University of Guelph, Guelph, Ontario, N1G 2W1, Canada.

C. Davison Ankney, Department of Zoology, University of Western Ontario, London, Ontario, N6A 5B7, Canada.