Geographic variation in nest-defence behaviour of the Red-tailed Hawk *Buteo jamaicensis*

RICHARD L. KNIGHT,[1,4] DAVID E. ANDERSEN,
MARC J. BECHARD[2] & N. VERNE MARR[3]
[1]*Department of Wildlife Ecology, University of Wisconsin, Madison, WI 53706, USA,*
[2]*Department of Biology, Boise State University, Boise, ID 83725, USA,* and
[3]*Ecosystems Department, Battelle-Northwest, PO Box 999, Richland, Washington
99352, USA.*

A close fit was found between the number of years since European settlement and the call and dive-rates of Red-tailed Hawks. Call-rates were highest in the most recently settled sites.

Anecdotal information suggests that some birds (e.g., Falconiformes, Charadriiformes) show geographic differences in nest-defence behaviour directed toward human beings (Williamson 1952, Newton 1979, Korpimäki 1986). Newton (1979) hypothesized that intraspecific differences in nest-defence behaviour of Falconiformes were due to past levels of human persecution. If persecution, e.g., shooting, disproportionately eliminated aggressive birds then nest-defence aggressiveness would vary with the history of persecution in an area (Newton 1979).

We examined Newton's hypothesis using the Red-tailed Hawk *Buteo jamaicensis* as our study animal. Red-tailed Hawks have been heavily persecuted (Baldwin *et al.* 1932, Kirkpatrick & Elder 1951) with population declines attributed to shooting in many areas (e.g., Howell 1932, Roberts 1932, Bromley 1944, Burleigh 1958). Henny & Wight (1972) determined that shooting pressure accounted for 10–24% of first-year mortality in Red-tailed Hawks, and they observed no change in shooting pressure over a 38 year period spanning 1926 to 1964.

Methods

Because the duration of persecution in different areas is difficult to estimate directly, we used length of settlement by Europeans as an index of duration of persecution. We used levels of present-day settlement as indices to the number of hawk/human interactions that might occur in a bird's lifetime. Thus we assumed the following: (1) length of European settlement is correlated positively with duration of persecution, (2) present-day density of human populations is correlated positively with intensity of persecution in a bird's lifetime, and (3) historical persecution by native North Americans was similar among areas (presumably, persecution by native North Americans was limited until acquisition of firearms from Europeans).

We measured nest-defence aggressiveness of Red-tailed Hawks in seven areas of North America. During 1983 we measured nest defence in four different study sites: West Virginia (38°50′N, 82°50′W),

[4] Present address: Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, Colorado 80523, USA.

Wisconsin (42°50′N, 89°30′W), Colorado (37°40′N, 103°50′W), and Washington (47°40′N, 119°38′W). In 1984 we measured nest defence in these same study sites (but at different territories) and at three additional sites: Idaho (43°10′N, 116°10′W), California (33°50′N, 117°50′W), and Saskatchewan, Canada (52°10′N, 107°10′W).

Time since European settlement in our study sites varied considerably. Beginning with the most recently settled site, years since European settlement were: Saskatchewan, Canada 75 years (Richards & Fung 1969), Washington 101 years (Burns et al. 1981), Colorado 107 years (Friedman 1985), Idaho 119 years (Lowell & Peterson 1976), Wisconsin 156 years (Durrie 1874), West Virginia 205 years (Ragland 1949), and California 215 years (Fages 1937).

Nests were visited when the young were between three and four weeks old (Petersen & Thompson 1977, Bechard et al. 1985) and when both adults were present. We approached nests slowly (1 m per s) and from a direction that made us clearly visible to the adults, avoiding days when it was windy (> 10 kmph), raining, or snowing. Data were collected only during the first visit to each nest to minimize alteration of the behaviour of adults by repeated visits (Knight & Temple 1986a, 1986b). Our operational measurements of 'aggressiveness' were call and dive rates and whether birds called or dived. While at the base of the nest tree or cliff, we recorded the number of calls and the number of dives of the hawk that came closest to us during a 10 minute period. A dive was considered as any downward break in horizontal flight.

Nest locations were plotted on aerial photographs and US Geological Survey maps, and the following measurements were taken: (1) distances to both the nearest paved highway and occupied home, and (2) the number of highways and occupied dwellings within a 1 km radius of the nest. To estimate human density, we randomly selected 20 sections (1 section = 2·5 km^2) in each study site from US Geological Survey maps and counted the number of occupied human dwellings; the total number of dwellings was then divided by 20.

Stepwise multiple-regression analyses were used to investigate the relationships between two response variables (i.e., call and dive rates) and six independent variables (length of European settlement, human density, and number and proximity of roads and homes to nests). We tested for relationships between study sites, proportion of birds calling, and proportion of birds diving with a log-linear model (Fienberg 1980). Multiple regression and model selection procedures follow those outlined in Snedecor & Cochran (1980) and Ryan et al. (1976).

Results

Rates of both calling and diving differed among the study sites (1-way anova, $F_{6,93} = 10·80$, $P < 0·001$, and $F_{6,93} = 5·64$, $P < 0·001$, respectively) (Table 1). Call-rates decreased monotonically with the highest call-rate in the most recently settled site (Saskatchewan) and the lowest call-rate in the study site settled the longest (California). Dive-rates were not as strongly related to time since settlement; but, in general, birds in study sites settled most recently had higher dive-rates than birds in study sites settled for longer times (Table 2). There were significant relationships between calls and study sites ($G_6 = 28·01$, $P < 0·001$) and dives and study sites ($G_6 = 36·38$, $P < 0·001$), indicating that both the proportion of birds that called and that dived varied between areas. Approximately half of the birds both called and dived in the study sites most recently settled whereas the remainder only called (Table 2). In the study sites settled the longest, very few birds dived; most birds either called or neither called nor dived.

Time since European settlement was the only explanatory variable in the final regression model selected for Red-tailed Hawk call-rates ($y = 110·1 − 0·47$ (length of settlement), $r^2 = 0·391$, $F_{1,98} = 62·88$, $P < 0·001$). Both length of human settlement and distance to the nearest home contributed to the regression model for dive-rates ($y = 3·3 − 0·019$ (length of settlement) $+ 0·00025$ (distance to home), $r^2 = 0·193$, $F_{2,97} = 11·62$, $P < 0·001$), with length of settlement (Pearson's partial correlation coefficient, $r = −0·342$, 97 df, $P < 0·001$) contributing more significantly than distance to home ($r = 0·268$, 97 df, $P < 0·01$). Human density, number and proximity of roads and the number of homes within a 1 km radius were not significant predictors in the final regression models.

Table 1. *Variations in call-rates and dive-rates of Red-tailed Hawks in seven areas of North America*

Location[1]	n	Mean ± s.d.	
		Calls/10 min	Dives/10 min
Saskatchewan	8	76·8 ± 28·0	2·3 ± 2·9
Washington	15	66·1 ± 19·2	1·4 ± 1·6
Colorado	24	59·0 ± 25·7	2·9 ± 3·2
Idaho	11	51·5 ± 28·3	1·1 ± 1·5
Wisconsin	25	30·9 ± 22·7	0·1 ± 0·3
West Virginia	9	16·8 ± 31·5	0·0
California	8	15·5 ± 21·1	0·6 ± 1·8

[1]Arranged in order of years since European settlement.

Table 2. *Frequencies of calling and diving among Red-tailed Hawks in seven areas of North America*

Location[1]	n	Percentage of birds that:		
		Called and dived	Only called	Neither called nor dived
Saskatchewan	8	62	38	0
Washington	15	47	53	0
Colorado	24	70	30	0
Idaho	11	45	55	0
Wisconsin	25	8	80	12
West Virginia	9	0	44	56
California	8	12	50	38

[1]Arranged in order of years since European settlement.

Discussion

Our results are consistent with Newton's (1979) hypothesis and suggest both natural selection and learning as mechanisms which alter nest-defence aggressiveness. Newton implied that natural selection was the mechanism that modified a species' nest-defence behaviour; however, he concluded that 'How much of these various behavioural differences result from natural selection and how much from learning is not known . . .' Natural selection is implicated because of the close fit between time since settlement and call and dive rates, and because the periods of time involved are so lengthy. Learning is weakly implicated because of the import effect that one contemporary variable (i.e., distance to the nearest occupied dwelling) had on dive-rates. Fitch *et al.* (1946) and Fitch (1958) noticed that encounters between Red-tailed Hawks and human nest intruders influenced subsequent behaviour toward humans. Our observations suggest that selective and learning pressures have affected the Red-tailed Hawk, mirroring to the regime of human activities within a geographical area. It would be interesting to compare nest-defence aggressiveness of adjacent populations of Red-tailed Hawks, one with and one without direct human persecution. Such a study would allow additional insights on the importance of learning in the absence of direct persecution (Knight 1984, Knight *et al.* 1987).

References

BALDWIN, S.P., KENDEIGH, S.C. & FRANKS, R.W. 1932. The protection of hawks and owls in Ohio. Ohio J. Sci. 32: 403–424.

BECHARD, M.J., ZOELLICK, B.W. & NICKERSON, M. 1985. Accuracy in determining the age of nestling Red-tailed Hawks. J. Wildl. Mgmt. 49: 226–228.

BROMLEY, S.W. 1944. The vanishing hawks. Sci. Month. 58: 373–376.

BURLEIGH, T.D. 1958. Georgia Birds. Norman, OK: University of Oklahoma Press.

BURNS, T., CLARKSON, M. MEANS, J., MUSIC, D. & WESSELMAN, R. 1981. Project Bunchgrass: an Historical Sketch of Bridgeport, Washington. Okanogan, WA: Okanogan County Historical Society.

DURRIE, D.S. 1874. History of Madison, the Capitol of Wisconsin; Including the Four Lake Country to July, 1874. Madison, WI: Atwood & Culver Printers.

FAGES, P. 1937. A Historical, Political, and Natural Description of California. Berkeley, CA: University of California Press.

FIENBERG, S.E. 1980. The Analysis of Cross-classified Categorical Data. Cambridge, MA: Massachusetts Institute of Technology Press.

FITCH, H.S. 1958. Home ranges, territories, and seasonal movements of vertebrates of the Natural History Reservation. University of Kansas Publ. 11: 63–326.

FITCH, H.S., SWENSON, F. & TILLOTSON, D.F. 1946. Behavior and food habits of the Red-tailed Hawk. Condor 48: 205–237.

FRIEDMAN, P.D. 1985. Final Report of History and Oral History Studies of the Fort Carson Pinon Canyon Maneuver Area, Las Animas County, Colorado. Denver, CO: Powers Elevation Corp.

HENNY, C.J. & WIGHT, H.M. 1972. Population ecology and environmental pollution: Red-tailed and Cooper's Hawks. In Population ecology of migratory birds: a symposium: 229–250. US Dept. Interior Res. Rept. 2.

HOWELL, A.H. 1932. Florida Bird Life. Florida Dept. Game and Fresh Water Fish & Bur. Biol. Survey, USDA, Washington, D.C.

KIRKPATRICK, C.M. & ELDER, W.H. 1951. The persecution of predaceous birds. Wilson Bull. 63: 138–140.

KNIGHT, R.L. 1984. Responses of nesting ravens to people in areas of different human densities. Condor 86: 345–346.

KNIGHT, R.L. & TEMPLE, S.A. 1986a. Why does intensity of avian nest-defense increase during the nesting cycle? Auk 103: 318–327.

KNIGHT, R.L. & TEMPLE, S.A. 1986b. Methodological problems in studies of avian nest defence. Anim. Behav. 34: 561–566.

KNIGHT, R.L., GROUT, D.J. & TEMPLE, S.A. 1987. Nest-defense behavior of the American Crow in urban and rural areas. Condor 89: 175–177.

KORPIMÄKI, E. 1986. Reversed size dimorphism in birds of prey, especially in Tengmalm's Owl *Aegolius funereus*: a test of the 'starvation hypothesis'. Ornis Scand. 17: 326–332.

LOWELL, H. & PETERSON, L. 1976. Our First Hundred Years. A Biography of the Lower Boise Valley, 1814–1914. Caldwell, ID: Caxton Printers.

NEWTON, I. 1979. Population Ecology of Raptors. Vermillion, SD: Buteo Books.

PETERSEN, L.R. & THOMPSON, D.R. 1977. Aging nestling raptors by 4th-primary measurements. J. Wildl. Mgmt 41: 587–590.

RAGLAND, H.C. 1949. History of Logan County from the files of the Logan Banner. Logan, WV: Logan Banner.

RICHARDS, J.H. & FUNG, K.I. (EDS). 1969. Atlas of Saskatchewan. Saskatoon, Saskatchewan: Univ. Saskatchewan.

ROBERTS, T.A. 1932. The Birds of Minnesota. Minneapolis, MN: University of Minnesota Press.
RYAN, T.A., JR., JOINER, B.L. & RYAN, B.F. 1976. Minitab student handbook. North Scituate, MA: Duxbury Press.
SNEDECOR, G.W. & COCHRAN, W.G. 1980. Statistical Methods (7th ed.). Ames, IA: Iowa State University Press.
WILLIAMSON, K. 1952. Regional variation in the distraction displays of the Oyster-catcher. Ibis 94: 85–96.