servation of the Marbled Murrelet. Gen. Tech.
Rep. PSW-GTR-152, Pacific Southwest Res. Sta.,
Forest Serv., U.S. Dept. Agriculture, Albany, CA.
RALPH, C. J., G. L. HUNT JR., M. G. RAPHAEL, AND J.
F. PIATT. 1995. Overview of the ecology and con-
servation of the Marbled Murrelet in North Amer-
ica, p. 3–22. *In* C. J. Ralph, G. L. Hunt Jr., M. G.
Raphael, and J. F. Piatt [EDS.], Ecology and con-
servation of the Marbled Murrelet. Gen. Tech.
Rep. PSW-GTR-152, Pacific Southwest Res. Sta.,
Forest Serv., U.S. Dept. Agriculture, Albany, CA.
RALPH, C. J., S. K. NELSON, M. M. SHAUGHNESSY, S.
L. MILLER, AND T. E. HAMER. 1994. Methods for
surveying Marbled Murrelets in forests. Pacific
Seabird Group, Marbled Murrelet Technical Com-
mittee, Tech. Paper No. 1. Oregon Co-operative
Wildl. Res. Unit, Oregon State Univ., Corvallis,
OR.
RIC (RESOURCES INVENTORY COMMITTEE). 1997. Stan-
dardized inventory methodologies for components
of British Columbia's biodiversity: Marbled Mur-
relets in marine and terrestrial habitats. Version
1.1. Publication No. 208, B.C. Resources Inven-
tory Committee, Ministry of Environment, Lands
and Parks, Victoria, B.C., Canada.
RODWAY, M. S., AND H. M. REGEHR. 1999. Inland in-
ventory: Marbled Murrelet activity and structural
characteristics of old-growth forests in Clayoquot
Sound, British Columbia, 1995–1997, p. 119–236.
In T. A. Chatwin, A. E. Burger, and L. E. Jones
[EDS.], Inventory of Marbled Murrelets in Clayo-
quot Sound, 1997. Unpublished report to B.C.
Ministry of Environment, Lands and Parks, Van-
couver Island Regional Office, Nanaimo, B.C.,
Canada.
RODWAY, M. S., J.-P. L. SAVARD, AND H. M. REGEHR.
1991. Habitat use and activity patterns of Marbled
Murrelets at inland and at-sea sites in the Queen
Charlotte Islands, British Columbia. Tech. Rep.
Ser. No. 122. Canadian Wildlife Service, Pacific
and Yukon Region, Delta, B.C., Canada.
VERBEEK, N. A. M., AND R. W. BUTLER. 1999. North-
western Crow (*Corvus caurinus*). *In* A. Poole and
F. Gill [EDS.], The birds of North America, No.
407. Birds of North America, Inc., Philadelphia.
ZAR, J. H. 1996. Biostatistical analysis. 3rd ed. Pren-
tice Hall, Upper Saddle River, NJ.

CORRELATES OF HARLEQUIN DUCK DENSITIES DURING WINTER IN PRINCE WILLIAM SOUND, ALASKA[1]

DANIEL ESLER

U.S. Geological Survey, Alaska Biological Science Center, 1011 E. Tudor Rd., Anchorage, AK 99503,
e-mail: daniel_esler@usgs.gov

TIMOTHY D. BOWMAN

U.S. Fish and Wildlife Service, 1011 E. Tudor Rd., Anchorage, AK 99503

THOMAS A. DEAN

Coastal Resources Associates, Inc., 1185 Park Center Dr., Suite A, Vista, CA 92083

CHARLES E. O'CLAIR

National Oceanographic and Atmospheric Administration, Auke Bay Laboratory, 11305 Glacier Highway,
Juneau, AK 99801

STEPHEN C. JEWETT

Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, AK 99775

LYMAN L. McDONALD

Western Ecosystems Technology, Inc., 2003 Central Ave., Cheyenne, WY 82001

Abstract. We evaluated relationships of Harlequin Duck (*Histrionicus histrionicus*) densities to habitat attributes, history of habitat contamination by the 1989 *Exxon Valdez* oil spill, and prey biomass density and abundance during winters 1995–1997 in Prince William Sound, Alaska. Habitat features that explained variation in duck densities included distance to streams and reefs, degree of exposure to wind and wave action, and dominant substrate type. After accounting for

these effects, densities were lower in oiled than un-oiled areas, suggesting that population recovery from the oil spill was not complete, due either to lack of recovery from initial oil spill effects or continuing del-eterious effects. Prey biomass density and abundance were not strongly related to duck densities after ac-counting for habitat and area effects. Traits of Harle-quin Ducks that reflect their affiliation with naturally predictable winter habitats, such as strong site fidelity and intolerance of increased energy costs, may make their populations particularly vulnerable to chronic oil spill effects and slow to recover from population re-ductions, which may explain lower densities than ex-pected on oiled areas nearly a decade following the oil spill.

Key words: density, Exxon Valdez oil spill, food, habitat, Harlequin Duck, Histrionicus histrionicus, population recovery.

Harlequin Ducks (Histrionicus histrionicus) are inex-tricably linked to nearshore marine environments dur-ing the nonbreeding portion of the annual cycle throughout their holarctic range. Adults leave coastal areas only for a few summer months when they mi-grate to fast-moving streams to nest and raise broods. Despite the importance of nearshore areas for Harle-quin Duck populations, fine-scale winter habitat asso-ciations rarely have been quantified.

In March 1989, the Exxon Valdez ran aground, spill-ing nearly 42 million liters of oil into Prince William Sound, a wintering area for approximately 14,000 Har-lequin Ducks. As much as 40% of the spilled oil was deposited in intertidal and shallow subtidal zones of Prince William Sound (Wolfe et al. 1994), the areas used by Harlequin Ducks. Although much of the oil degraded and dissipated within a few years of the spill, some residual oil was still present in these areas through at least 1997 (Hayes and Michel 1999). Im-mediate bird mortality from the Exxon Valdez oil spill was high (Piatt et al. 1990) and more than 1,000 Har-lequin Ducks were estimated to have died as an im-mediate and direct result of the spill (J. Piatt, U.S. Geological Survey, pers. comm.). Furthermore, there have been concerns about continued effects of the Exxon Valdez oil spill on Harlequin Duck populations and lack of full population recovery (Esler et al. 2000).

We studied Harlequin Duck habitat associations in Prince William Sound during winter to identify envi-ronmental variables that relate to Harlequin Duck den-sities and to assess the status of Harlequin Duck pop-ulations following the Exxon Valdez oil spill. Evalua-tion of Harlequin Duck population recovery from the oil spill has been constrained by a paucity of prespill data from winter, the season of highest abundance of Harlequin Ducks in Prince William Sound and likely the period of formation of core subpopulations from a population structure perspective (Cooke et al. 2000). For this study, we adopted a control-impact study de-sign to assess potential oil spill effects, in which we compared densities of Harlequin Ducks between oiled and unoiled areas, recognizing the need to control for intrinsic area differences (Wiens and Parker 1995). Lower densities than expected on oiled areas (after ac-counting for other environmental factors) could result

from either failure to recover from immediate popu-lation impacts or from continuing deleterious effects of the spill; either case would lead to an interpretation of lack of full population recovery.

METHODS

STUDY AREA

Study locations were within oiled and unoiled areas of Prince William Sound, Alaska. The oiled study area included 75.7 km of shoreline within two bays on Knight Island, Herring Bay and Bay of Isles, which were heavily oiled by the Exxon Valdez spill. The un-oiled area was 74.1 km of shoreline in the Stockdale Harbor and Port Chalmers region of northwestern Montague Island, selected because of the close prox-imity to the oil spill zone.

Analyses of habitat associations were based on mea-surement of habitat attributes and Harlequin Duck den-sities at sampling sites within each study area. To se-lect sites, the shoreline of each study area was divided into contiguous 200-m sections. From randomly se-lected start points, 216 sections (113 on Knight Island and 103 on Montague Island) were then systematically selected as sampling sites, resulting in coverage throughout each study area.

HARLEQUIN DUCK SURVEYS

We surveyed Harlequin Duck numbers and distribution during 4–12 December 1995, 12–24 February 1996, 4–14 December 1996, and 14–23 February 1997, com-pleting five replicates on Knight Island and seven on Montague Island. Surveys were conducted by boat with a two- or three-person team consisting of an op-erator/observer and at least one observer/data recorder. For all Harlequin Ducks observed within 200 m of the study area shoreline, we recorded flock sizes and mapped locations on mylar overlays of 1:15,000 aerial photos.

To estimate Harlequin Duck densities associated with each sampling site, we calculated the number of ducks detected during shoreline censuses within 200-m linear shoreline distance of the midpoint of each sampling site. Duck densities were expressed as the average number of birds associated with the sampling site over all replicate surveys. Harlequin Duck num-bers were consistent across surveys (CV = 4.1% on Montague Island and 8.0% on Knight Island) and Har-lequin Duck site fidelity is high (Robertson et al. 1999, Cooke et al. 2000), suggesting that average densities should be a robust indicator of Harlequin Duck use of each site. Replication and duration of surveys resulted in data collection over a range of tidal states and weather conditions in both areas, and thus any varia-tion potentially related to these factors should not in-fluence inter-area comparisons.

HABITAT ATTRIBUTES

At each site, we measured several habitat variables, including: exposure—a description of wind and wave action, categorized as full exposure, partial exposure, and not exposed; dominant substrate—categorized as rocky (bedrock and boulder areas) and mixed (uncon-solidated, i.e., various mixtures of sand, pebbles, and cobble); distance to stream mouth—straight line dis-

tance from the midpoint of the sampling site to nearest stream mouth categorized as <200 m, 200–500 m, >500–1,000 m, and >1,000 m; distance to reef—straight line distance from the midpoint of the sampling site to the nearest offshore reef (defined as covered at high tide but exposed at lower tides) categorized as 200–500 m, >500–1,000 m, and >1,000 m; and intertidal slope—the average slope (in degrees) of the mussel zone. Observations with missing data for a habitat variable were excluded from habitat association models that included that variable.

HABITAT ASSOCIATION MODELS

We conducted general linear model analyses to assess relationships of habitat attributes (explanatory variables) to average Harlequin Duck densities (the response variable), using each sampling site as an observation. Scatterplots of Harlequin Duck densities by habitat and food variables indicated that distributions violated the assumption of linearity; square-root transformation of Harlequin Duck densities resolved this problem. Categorical variables were included as a set of indicator variables, with one level of each variable designated as the reference level and, thus, not included in model selection procedures (Ramsey and Schafer 1997).

To select the model from which we drew inference, we used Mallow's C_p values to contrast all possible combinations of explanatory variables. Explanatory variables included all habitat parameters, their interactions with area, and an area (oiling history) term. This method of model selection uses the principle of parsimony to determine which model is best fit by the data (Burnham and Anderson 1998), avoiding assumptions and biases of traditional stepping (i.e., forward, backward, and stepwise) model selection procedures (Flack and Chang 1987). Using this approach to model selection, the model with the lowest C_p value is the one best supported by the data and, thus, provides the strongest inference. We interpreted inclusion of a given parameter in a selected model as evidence that the parameter was related to Harlequin Duck densities, after accounting for effects of other included parameters. Inclusion of the area term in the best-fitting model would suggest that oiling history was related to Harlequin Duck densities after accounting for any effects of habitat attributes and differences in effects of habitat attributes between areas.

THE ROLE OF FOOD

Harlequin Ducks in marine areas eat intertidal and shallow subtidal benthic invertebrates, particularly amphipods, limpets, snails, chitons, and mussels (Goudie and Ankney 1986). We sampled Harlequin Duck prey in each area at a systematically selected subset of 15 of the sampling sites. Because of generally low densities of Harlequin Ducks on Knight Island, four additional sites with relatively higher Harlequin Duck densities were selected to ensure that sampling represented the full range of Harlequin Duck densities. Similarly, four sites with moderate to low duck densities were added on Montague Island.

To sample intertidal blue mussels (*Mytilus trossulus*), we removed all mussels from within 10 500-cm^2 quadrats placed in the mussel zone of each site. Ash-

free dry mass of each mussel 5–25 mm in length was estimated based on predictive equations of biomass by length (Holland-Bartels 2000). Samples of other invertebrate prey (limpets, chitons, lacunid snails, littorine snails, other snails, amphipods, and other crustaceans) were obtained at six intertidal and shallow subtidal locations within each prey sampling site. All epifauna were removed from a 0.25-m^2 quadrat at each location. Ash-free dry weights of each prey item <25 mm in length were determined using a muffle furnace.

For data analyses, prey data were included in four forms: total food biomass density—the combined average biomass densities (g per 100 m^2) of mussels and other prey items; total food abundance—an estimate of the biomass (kg ash-free dry mass) of all food types within the 200-m sampling site, based on expansion of food biomass densities to the prey sampling areas; food biomass density without mussels—we also used biomass density estimates excluding mussels because biomass estimates of mussels were considerably higher (usually more than an order of magnitude) than other prey types, yet they constitute a relatively small part of the diet of Harlequin Ducks; and food abundance without mussels—similarly, we used prey abundance estimates excluding mussels.

To examine effects of prey on Harlequin Duck distributions, we assessed additional variation in duck densities related to food variables after accounting for habitat and area effects. We regressed residuals (observed Harlequin Duck densities–predicted densities) from the best-fitting habitat association model against the four measures of prey abundance and density.

RESULTS

Harlequin Duck densities were considerably higher at unoiled Montague Island (3.0 ± 0.2; average ducks per 400 m shoreline ± SE) than at oiled Knight Island (0.6 ± 0.1). Some aspects of the habitat were distinctly different between Montague and Knight Islands, including intertidal slope (5.8 ± 0.4 and 25.5 ± 1.7 degrees, respectively) and dominant substrate (37.9% and 73.5% rocky, respectively). On both areas, Harlequin Ducks were almost always observed in intertidal and shallow subtidal habitats very close to shore.

HABITAT ASSOCIATION MODELS

In the best-fitting model (Table 1), Harlequin Duck densities were positively related with having an offshore reef within 500 m, a stream within 200 m, and full exposure. The main effect of mixed substrate also had a positive parameter estimate, although there was a larger negative interaction of area by mixed substrate, suggesting that Harlequin Duck densities were positively associated with mixed substrate on Montague Island and negatively associated on Knight Island (Table 1). The rest of the top five models (those with the next four lowest Mallow's C_p values) also included the terms from the best-fitting model, indicating their importance for explaining variation in Harlequin Duck densities.

EFFECTS OF HISTORY OF OIL CONTAMINATION

The area term was included in the best-fitting model and had a large, negative parameter estimate (Table 1). In other words, duck densities were lower on oiled

TABLE 1. Results of general linear model analyses to evaluate relationships of Harlequin Duck densities (square-root transformed) in Prince William Sound, Alaska, winters 1995–1997, with habitat attributes and history of oil contamination by the 1989 *Exxon Valdez* oil spill. The parameter estimates (± SE) are from the best-fitting model, based on comparisons of all possible combinations of habitat attribute variables, habitat by area interactions, and an area (history of oil contamination) term.

Response variable	R^2	Explanatory variable	Parameter estimate
Ducks per 400 m	0.45	Intercept	1.17 ± 0.12
		Reef 200-500 m[a]	0.51 ± 0.15
		Stream 0-200 m[a]	0.34 ± 0.14
		Full exposure[a]	0.45 ± 0.12
		Mixed substrate[a]	0.32 ± 0.14
		Mixed substrate $\times$ Area[b]	-0.48 ± 0.18
		Area[b]	-0.69 ± 0.12

[a] Parameter estimate is in relation to all other levels of the categorical variable.
[b] Reference value for area is unoiled Montague Island; parameter estimates are interpreted as effects on oiled Knight Island.

Knight Island than unoiled Montague Island (the reference level for the area term) after accounting for effects of habitat attributes and differences in these attributes between areas, which we interpret as evidence that history of oil contamination was related to Harlequin Duck densities. All of the top five models included the area term. Also, a more complicated analysis of our data, in which the area term was added after selection of models including only habitat variables, found an exactly concordant result—oiling history was strongly and negatively related to Harlequin Duck densities (Holland-Bartels 2000).

THE ROLE OF FOOD

Duck density residuals were not related to total food abundance ($R^2 < 0.01$, $F_{1,30} = 0.02$, $P = 0.89$), total food biomass density ($R^2 < 0.01$, $F_{1,31} = 0.03$, $P = 0.87$), or food abundance without mussels ($R^2 = 0.04$, $F_{1,36} = 1.52$, $P = 0.23$). Food biomass density without mussels was positively correlated with duck density residuals ($R^2 = 0.17$, $F_{1,37} = 7.83$, $P = 0.01$). However, the amount of variation explained was low and the relationship was highly influenced by a single obser-
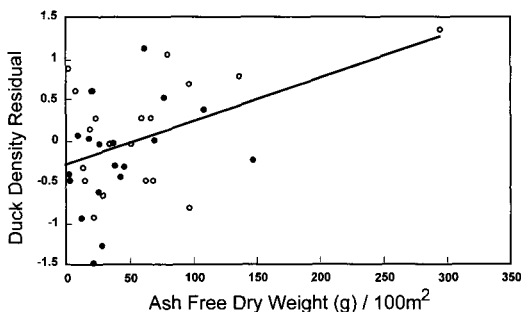

FIGURE 1. Linear relationship of residuals of Harlequin Duck densities (ducks/400 m shoreline; square-root transformed) from a general linear model of habitat associations against prey biomass density. Empty circles represent Knight Island (oiled) study sites and solid circles represent Montague Island (unoiled) sites.

vation (Fig. 1), a site on oiled Knight Island that was nonsystematically selected to represent high duck densities and which also had high densities of subtidal foods (especially snails and amphipods); without this observation, the relationship was nonsignificant ($R^2 = 0.07$, $F_{1,36} = 2.62$, $P = 0.11$). Taken together, these analyses suggest that variation in food explained little variation in duck densities beyond that explained by habitat attributes.

DISCUSSION

HABITAT RELATIONS TO HARLEQUIN DUCK WINTER DENSITIES

We assume that habitat associations of Harlequin Ducks that we observed were related to habitat profitability and reflected, to some degree, solutions to the optimization process of balancing benefits of habitats against detrimental aspects (Abrahams and Dill 1989, Guillemette et al. 1993). This balance is influenced by ecological characteristics of the species (Hilden 1965), which in the case of Harlequin Ducks include a life history requirement for high winter survival and high levels of winter philopatry.

Few other studies have quantified winter Harlequin Duck habitat associations. Goudie and Ankney (1988) documented that Harlequin Ducks were closer to shore and used reefs more than other sea duck species in Newfoundland. Harlequin Duck winter habitats have been qualitatively characterized and consistently described as being very close to shore and in a varied mix of substrates (Vermeer 1983), in agreement with our findings. We found strong positive relationships between Harlequin Duck densities and full exposure, occurrence of nearby streams, and occurrence of nearby reefs. Presence of a stream may influence prey distribution and provide fresh water to reduce osmotic stress for birds that ingest salts while feeding on marine invertebrates (Nyström and Pehrsson 1988). Reefs likely serve as safe resting sites and also offer intertidal foraging opportunities.

Harlequin Duck habitat use and life history are inextricably linked. Among ducks, Harlequin Ducks are relatively long-lived and have low and variable annual productivity (Goudie et al. 1994), a life history that

requires high survival. High survival, in turn, depends on selection of stable and predictable habitats. On a broad scale, coastal habitats are thought to offer more stable wintering environments for waterfowl than inland sites (Diefenbach et al. 1988). Within coastal habitats, Harlequin Ducks occupy the productive intertidal and shallow subtidal zones. Goudie and Ankney (1986) described Harlequin Ducks as living near an energetic threshold as a result of their small body size and relatively harsh wintering environments. Consequently, Harlequin Ducks must forage nearly continuously during daylight hours of winter (Goudie and Ankney 1986). The habitat associations that we documented are consistent with this foraging strategy. Use of shallow water reduces dive and search times for more efficient foraging (Guillemette et al. 1993). Use of areas near streams and reefs may reduce energetic costs and time of transit between foraging areas and other resources (e.g., fresher water, roost sites). In summary, Harlequin Ducks must use habitats that predictably allow them to meet daily energy costs within their time-limited foraging regime, while minimizing risk of mortality in concordance with their life history requirement for high survival probabilities.

EFFECTS OF HISTORY OF OIL CONTAMINATION

We found that after accounting for effects of habitat attributes, history of oil contamination from the *Exxon Valdez* spill was related to Harlequin Duck densities, with densities lower on oiled Knight Island than would be predicted based on the habitat attributes that we measured. Our data were consistent with a hypothesis that Harlequin Duck populations were not fully recovered from the oil spill.

Evidence from other studies supports a hypothesis that Harlequin Duck populations experienced continued effects of the *Exxon Valdez* oil spill during the course of this study. Trust et al. (2000) concluded that Harlequin Ducks and the ecologically similar Barrow's Goldeneye (*Bucephala islandica*) continued to be exposed to oil through 1998, as indicated by higher induction of cytochrome P450 1A in oiled areas than unoiled areas. Also, Harlequin Duck adult female survival during winters 1995–1998 was lower on oiled areas than unoiled areas (Esler et al. 2000), and laboratory studies support logical links between reduced survival rates and oil exposure (Holmes et al. 1979). Because population dynamics of birds with life histories like Harlequin Ducks are particularly sensitive to variation in adult female survival (Goudie et al. 1994, Schmutz et al. 1997), lower survival on oiled areas may have led to population declines (Rosenberg and Petrula 1998) and hence lower densities on oiled areas than predicted, as found in this study. Harlequin Duck populations have relatively low intrinsic growth rates (Goudie et al. 1994), so full recovery (i.e., duck densities at levels predicted from intrinsic habitat attributes) likely will not occur until long after deleterious effects of the oil spill have ceased.

Day et al. (1997) studied habitat use by birds in Prince William Sound during the period immediately following the *Exxon Valdez* spill (1989–1991) and found no oil spill effects on Harlequin Ducks during winter. Why were our results different from those of Day et al. (1997)? First, because deleterious effects of the oil spill continued through the period of our study and until at least 1998 (Rosenberg and Petrula 1998, Esler et al. 2000, Trust et al. 2000), differences in Harlequin Duck abundance relative to oil contamination may have been more pronounced during our study than during the study of Day et al. (1997). Also, Day et al. (1997) used bays as sampling units and characterized habitats at the scale of the entire bay, presumably by necessity due to their broader study question to look at all marine birds over a wider geographic area. Our study demonstrated that Harlequin Ducks respond to much smaller scale variations in habitat attributes. Harlequin Ducks exhibit high fidelity to specific shoreline segments (Robertson et al. 1999, Cooke et al. 2000), therefore, we were able to account for differences in environmental attributes at the scale that Harlequin Ducks select habitats before testing for relationships to history of oil contamination, allowing for a finer scale and presumably more powerful test.

THE ROLE OF FOOD

Food may influence the distribution and abundance of some sea ducks (Nilsson 1972, Guillemette et al. 1993). In the context of the *Exxon Valdez* oil spill, strong relationships between Harlequin Duck densities and food would indicate food limitation as a possible mechanism for lack of population recovery. However, we found that food explained little variation in duck densities beyond habitat attributes and area effects.

Foraging characteristics of Harlequin Ducks suggest that they may be more time-limited than food-limited. Energetic requirements of this small-bodied sea duck necessitate nearly continuous feeding during daylight hours of winter and a generalist diet that includes many common benthic invertebrates (Goudie and Ankney 1986). This foraging strategy, particularly in association with high levels of winter site fidelity (see below), suggests that food may be predictably abundant, and the crux for Harlequin Ducks is to maximize energy intake during a short daily foraging period. Other authors (Nilsson 1972) have found that food exploitation by some wintering diving ducks was small relative to standing crop; we suggest that this is likely the case for Harlequin Ducks.

SIGNIFICANCE OF PHILOPATRY

A growing body of data suggests that Harlequin Ducks exhibit high philopatry throughout their annual cycle (Cooke et al. 2000, Robertson et al. 2000). Harlequin Duck winter habitat use is likely influenced by strong philopatry (Cooke et al. 2000), which reflects high stability of nearshore environments coupled with advantages of philopatry, including site familiarity and interannual pair reunion (Robertson and Cooke 1999, Smith et al. 2000).

From the perspective of oil spill recovery, high winter philopatry suggests that if residual oil spill damages exist, birds from oiled areas are vulnerable to chronic and cumulative spill effects as they return to those areas each year. Also, if dispersal and movements among areas are limited, recovery of groups of birds in oiled areas must occur largely through production and recruitment specific to that group and numbers are not bolstered through immigration. Lower densities than

expected on oiled areas detected in this study may be a result of one or both of these processes.

LITERATURE CITED

ABRAHAMS, M. V., AND L. M. DILL. 1989. A determination of the energetic equivalence of the risk of predation. Ecology 70:999–1007.

BURNHAM, K. P., AND D. R. ANDERSON. 1998. Model selection and inference: a practical information theoretic approach. Springer-Verlag, New York.

COOKE, F., G. J. ROBERTSON, C. M. SMITH, R. I. GOUDIE, AND W. S. BOYD. 2000. Survival, emigration, and winter population structure of Harlequin Ducks. Condor 102:137–144.

DAY, R. H., S. M. MURPHY, J. A. WIENS, G. D. HAYWARD, E. J. HARNER, AND L. N. SMITH. 1997. Effects of the *Exxon Valdez* oil spill on habitat use by birds in Prince William Sound, Alaska. Ecol. Appl. 7:593–613.

DIEFENBACH, D. R., J. D. NICHOLS, AND J. E. HINES. 1988. Distribution patterns during winter and fidelity to wintering areas of American Black Ducks. Can. J. Zool. 66:1506–1513.

ESLER, D., J. A. SCHMUTZ, R. L. JARVIS, AND D. M. MULCAHY. 2000. Winter survival of adult female Harlequin Ducks in relation to history of contamination by the *Exxon Valdez* oil spill. J. Wildl. Manage. 64:839–847.

FLACK, V. F., AND P. C. CHANG. 1987. Frequency of selecting noise variables in subset regression analysis: a simulation study. Am. Stat. 41:84–86.

GOUDIE, R. I., AND C. D. ANKNEY. 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. Ecology 67:1475–1482.

GOUDIE, R. I., AND C. D. ANKNEY. 1988. Patterns of

habitat use by sea ducks wintering in southeastern Newfoundland. Ornis. Scand. 19:249–256.

GOUDIE, R. I., S. BRAULT, B. CONANT, A. V. KONDRATYEV, M. R. PETERSEN, AND K. VERMEER. 1994. The status of sea ducks in the North Pacific rim: toward their conservation and management. Trans. N. Am. Wildl. Nat. Res. Conf. 59:27–49.

GUILLEMETTE, M., J. H. HIMMELMAN, AND C. BARETTE. 1993. Habitat selection by Common Eiders in winter and its interaction with flock size. Can. J. Zool. 71:1259–1266.

HAYES, M. O., AND J. MICHEL. 1999. Factors determining the long-term persistence of *Exxon Valdez* oil in gravel beaches. Marine Poll. Bull. 38:92–101.

HILDEN, O. 1965. Habitat selection in birds—a review. Ann. Zool. Fenn. 2:53–75.

HOLLAND-BARTELS, L. E. [ED.]. 2000. Mechanisms of impact and potential recovery of nearshore vertebrate predators following the 1989 *Exxon Valdez* oil spill. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 99025), U.S. Geol. Surv., Alaska Biol. Sci. Center, Anchorage, AK.

HOLMES, W. N., J. GORSLINE, AND J. CRONSHAW. 1979. Effects of mild cold stress on the survival of seawater-adapted Mallard ducks (*Anas platyrhynchos*) maintained on food contaminated with petroleum. Environ. Res. 20:425–444.

NILSSON, L. 1972. Habitat selection, food choice, and feeding habits of diving ducks in coastal waters of south Sweden during the non-breeding season. Ornis Scand. 3:55–78.

NYSTRÖM, K. G. K., AND O. PEHRSSON. 1988. Salinity as a constraint affecting food and habitat choice of mussel-feeding diving ducks. Ibis 130:94–110.

PIATT, J. F., C. J. LENSINK, W. BUTLER, M. KENDZIOREK, AND D. R. NYESWANDER. 1990. Immediate impact of the "Exxon Valdez" oil spill on marine birds. Auk 107:387–397.

RAMSEY, F. L., AND D. W. SCHAFER. 1997. The statistical sleuth: a course in methods of data analysis. Wadsworth, Belmont, CA.

ROBERTSON, G. J., AND F. COOKE. 1999. Winter philopatry in migratory waterfowl. Auk 116:20–34.

ROBERTSON, G. J., F. COOKE, R. I. GOUDIE, AND W. S. BOYD. 1999. Within-year fidelity of Harlequin Ducks to a moulting and wintering area, p. 53–60. *In* R. I. Goudie, M. R. Petersen, and G. J. Robertson [EDS.], Behaviour and ecology of sea ducks. Can. Wildl. Serv. Occ. Paper Series No. 100, Ottawa, Ontario, Canada.

ROBERTSON, G. J., F. COOKE, R. I. GOUDIE, AND W. S. BOYD. 2000. Spacing patterns, mating systems, and winter philopatry in Harlequin Ducks. Auk 117:299–307.

ROSENBERG, D. H., AND M. J. PETRULA. 1998. Status of Harlequin Ducks in Prince William Sound, Alaska, after the *Exxon Valdez* oil spill, 1995–97. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 97427), Alaska Dept. Fish Game, Div. Wildl. Conserv., Anchorage, AK.

SCHMUTZ, J. A., R. F. ROCKWELL, AND M. R. PETERSEN. 1997. Relative effects of survival and reproduc-

tion on population dynamics of Emperor Geese. J. Wildl. Manage. 61:191–201.

SMITH, C. M., F. COOKE, G. J. ROBERTSON, R. I. GOU-DIE, AND W. S. BOYD. 2000. Long-term pair bonds in Harlequin Ducks. Condor 102:201–205.

TRUST, K. A., D. ESLER, B. R. WOODIN, AND J. J. STE-GEMAN. 2000. Cytochrome P450 1A induction in sea ducks inhabiting nearshore areas of Prince William Sound, Alaska. Marine Poll. Bull. 40: 397–403.

VERMEER, K. 1983. Diet of the Harlequin Duck in the Strait of Georgia, British Columbia. Murrelet 64: 54–57.

WIENS, J. A., AND K. R. PARKER. 1995. Analyzing the effects of accidental environmental impacts: approaches and assumptions. Ecol. Appl. 5:1069–1083.

WOLFE, D. A., M. J. HAMEEDI, J. A. GALT, G. WATA-BAYASHI, J. SHORT, C. O'CLAIR, S. RICE, J. MICH-EL, J. R. PAYNE, J. BRADDOCK, S. HANNA, AND D. SALE. 1994. The fate of the oil spilled from the *Exxon Valdez*. Environ. Sci. Technol. 28:561–568.

INFLUENCE OF FEMALE AGE AND BODY MASS ON BROOD AND DUCKLING SURVIVAL, NUMBER OF SURVIVING DUCKLINGS, AND BROOD MOVEMENTS IN REDHEADS[1]

TINA YERKES[2]

Department of Zoology, University of Manitoba, Winnipeg, MB R3T 2N2, Canada

Abstract. I documented brood and duckling survival, the number of surviving ducklings, and brood movements of Redheads, and examined the association between these variables and female age and body mass. Redhead brood success was 55% and duckling daily survival rates averaged 0.868. Female body mass, but not age, was related to brood and duckling survival and the number of surviving ducklings. Successful females were heavier and produced more ducklings. All brood-movement measures differed between successful and unsuccessful females, however, the distance of the first move between wetlands accounted for the most variability in brood success. Increased body mass, but not age, was associated with longer first brood movements.

Key words: Aythya americana, body mass, brood movements, brood survival, duckling survival, female age, Redhead.

Although North American Anatinae produce precocial young, females provide post-hatch care. Poor or reduced brood care may result in lower brood or duckling survival (Talent et al. 1983). Among ducks, several factors may affect individual variation in brood care: temporal variation, brood age and size, and adult age and body mass. Older parents, as compared to yearlings, should maximize fitness by exhibiting greater parental investment (PI) (Trivers 1974). Older parents may also benefit from experience gained through raising previous broods, and thus have higher brood success than younger parents. Afton (1984) provided weak support for increased PI with age in Lesser Scaup (*Aythya affinis*) because the amount of time females spent in brood care increased with age to a point. Female age did not influence brood survival in Lesser Scaup (Afton 1984) or Canvasbacks (*Aythya valisineria*) (Serie et al. 1992).

Female body mass may further influence variation in PI and has been shown to influence incubation (Gloutney and Clark 1991, Yerkes 1998) and brood adoption or abandonment (Kehoe 1986) in ducks. Only one study, however, examined the relationship between female body mass and brood survival, but detected no relationship of these variables in Canvasbacks or Redheads (*Aythya americana*) (Arnold et al. 1995).

Brood movements among wetlands may affect brood survival and could be influenced by female age and body mass, although these have not been examined to date. Females may move their broods in response to low invertebrate numbers or to avoid wetlands lacking a zone of emergent vegetation. Results from studies examining the relationship between brood movements and brood survival are conflicting: some demonstrate a negative relationship (Rotella and Ratti 1992a), whereas others found a positive or no relationship (Mauser et al. 1994).

Little is known about Redhead brood survival or