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EFFECT OF FOOD AVAILABILITY ON ARRIVAL AND DEPARTURE DECISIONS OF HARLEQUIN DUCKS AT DIURNAL FEEDING GROUNDS

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Abstract. We investigated three types of decisions made by Harlequin Ducks (*Histrionicus histrionicus*) in moving between nearshore feeding and offshore resting areas: when to move, whether to move synchronously, and whether to form dense flocks on the roosting grounds. We used the spawning of Pacific herring (*Clupea pallasi*) as a natural food-supplementation experiment. Birds arrived at nearshore feeding areas a few minutes later and departed almost an hour earlier relative to sunrise and sunset when spawn was available than before and after. Cloud cover and high winds resulted in earlier departures, especially during spawning. Arriving, departing, and offshore groups consisted most frequently of two ducks, and birds showed little tendency to synchronize movements or to form dense flocks when resting. Results indicate that Harlequin Ducks avoid crepuscular and nocturnal periods near shore when not constrained by food availability and the length of daylight in which to feed.

Key words: Clupea pallasi, *daily movements, flexible time budgets, food availability, Harlequin Duck, herring spawn,* Histrionicus histrionicus.

Efecto de la Disponibilidad de Alimento en las Decisiones de Arribo y Partida de *Histrionicus histrionicus* en Áreas de Alimentación Diurna

Resumen. Investigamos tres tipos de decisiones hechas por *Histrionicus histrionicus* (Pato Arlequín) al moverse entre áreas de alimentación cercanas a la costa y áreas de reposo mar adentro: cuándo moverse, si se mueven de modo sincrónico, y si forman bandadas densas en las áreas de reposo. Utilizamos el desove del arenque del Pacífico (*Clupea pallasi*) como un experimento de suplemento de alimento natural. En relación al amanecer y anochecer, las aves llegaron a las áreas de alimentación cercanas a la costa unos minutos después y se fueron casi una hora más temprano cuando los huevos de peces estuvieron disponibles que cuando no lo estuvieron, ya sea antes o después. Cobertura de nubes y fuertes vientos trajeron aparejadas partidas más tempranas, especialmente durante la etapa de desove. Los grupos que llegaban, partían y los que se encontraban mar adentro estuvieron en su mayoría conformados por dos patos, y las aves en general no tendieron a sincronizar sus movimientos o a formar grupos densos durante el reposo. Los resultados indican que *H. histrionicus* evita permanecer cerca de la costa durante períodos crepusculares y nocturnos cuando no se haya limitado por la disponibilidad de alimentos y por la cantidad de horas de luz para alimentarse.

Individuals may trade off predation risk against nutritional state when making foraging decisions (Lima and Dill 1990). Changes in food availability can alter cost-benefit ratios and make animals more or less willing to risk predation. Reducing predation risk is thought to explain why many waterfowl species undertake daily movements between feeding and safer resting grounds, and why they often form dense flocks on roosting grounds (Fox et al. 1994, Cox and Afton 1996). Decisions of when and how to move to and from feeding areas are likely affected by a suite of factors, including foraging method, prey type, nutri-

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tional state, food availability, environmental conditions, and predation risk (Nilsson 1970, Miller 1985, Cox and Afton 1996). Effects of food availability have not previously been investigated.

For diurnal foragers in northern latitudes, decreased daylight during winter exerts constraints on time budgets that can affect survival, habitat use, and winter distribution (Goudie and Ankney 1986, Guillemette et al. 1992). In addition, prevalent cloudy conditions in winter reduce light levels, further limiting diurnal time available for feeding. Birds may compensate for shorter daylight by increasing the proportion of the day spent feeding (Nilsson 1970, Goudie 1999) and increasing the rate of food processing (Guillemette 1998). They may also extend the time available for feeding by arriving earlier, leaving later, or feeding nocturnally (Nilsson 1970, Brown and Fredrickson 1997).

Studies investigating daily movements are generally observational because it is difficult to manipulate factors affecting movements under natural conditions. Spawning by Pacific herring (*Clupea pallasi*) along the British Columbia coast provides a superabundant food resource available to waterbirds for about three weeks in late winter–early spring (Haegele 1993). We used it as a natural food-supplementation experiment to investigate how arrival and departure behavior of Harlequin Ducks (*Histrionicus histrionicus*) is affected by food availability.

Harlequin Ducks forage diurnally along rocky, marine shorelines and move to offshore waters at night (Phillips 1925, Fleischner 1983). During winter they spend the majority of daylight hours feeding (Goudie and Ankney 1986). The influx of herring spawn relaxes constraints on foraging time, and birds spend less than half as much time foraging when spawn is available than during the months before and after (MSR, unpubl. data).

We investigated three types of decisions made by Harlequin Ducks in moving between feeding and resting areas: when to move, whether to move synchronously, and whether to form dense flocks on the roosting grounds. We hypothesized that arrivals near shore should be later and departures earlier during herring spawning if offshore resting areas offer decreased predation risk and are preferred by satiated birds. Secondly, if birds are at risk from aerial predators during flights onshore and offshore, then synchronicity in behavior may be important (Gochfeld 1980). If differences in foraging efficiency among birds are minimized when food is abundant, then arrivals and departures should be more synchronous during spawning than at other times. Finally, we hypothesized that birds will form dense flocks offshore at all times if there is predation risk there. We compared arrival and departure behavior before, during, and after the herring spawning period. Effects of weather were investigated to ensure that seasonal differences were not simply due to different weather conditions (Cox and Afton 1996).

A secondary objective of this study addressed a widely accepted assumption in time-budget methodology. Activity budgets are usually determined by scan or focal animal sampling from which proportions of time spent in various activities can be estimated (Altmann 1974). Multiplying the proportion of time spent by total time available then provides estimates of absolute times spent in specific behaviors. The hours between sunrise and sunset are often used as a reasonable surrogate for the time available for feeding by diurnally foraging birds (e.g., Guillemette 1998). We determined seasonal changes in arrival and departure times relative to sunrise and sunset, and whether Harlequin Ducks ever foraged at night, to evaluate the accuracy of using daylight hours as a measure of the time available for feeding.

METHODS

The study was conducted along the northeast shore of Hornby Island (49°33′N, 124°40′W), an important molting and wintering site for Harlequin Ducks and part of the main spawning grounds for herring in the Strait of Georgia, British Columbia, Canada (Haegele 1993). Open water extends 16 km northeast and over 30 km northwest and southeast off the study area. Evening and morning observations were made during February through April in 1998 and 1999 and from November 1999 to April 2000. Observations of offshore groups were made by telescope from shore at dusk and dawn when the sea was calm and visibility was good, and by binoculars from a kayak at sea in the evening and after dark under starlight or moonlight when birds were visible at close range. Distances offshore were estimated by comparison to landmarks.

We determined whether birds stayed into the night or were present before dawn on 88 and 71 days, respectively. Arrivals and departures were determined during 36 observation sessions, 2–4 hr long, usually paired on the same day or night. Flock size and number were counted during each minute interval between the times of the first and last flocks to arrive or depart. Group sizes near shore were much larger during spawning than at other times, and numbers of birds sampled per observation session ranged from 4–58 during winter, 1656–3172 during spawning, and 14–283 in spring. Birds on the water were considered members of different groups if >10 m separated them. Percent cloud cover was recorded. We estimated wind speed using the Beaufort scale of wind force. Sunrise and sunset times for the study area were obtained from the U.S. Naval Observatory Astronomical Applications Data Services (U.S. Navy 2000).

Data were compared among three date categories: winter (November to February), spawning (the three-week period after herring first spawned in early March), and spring (April), two cloud categories (0–89% and $\geq$90% cloud cover), three wind direction categories (no wind, southerly winds, and northerly winds), and three wind speed categories (0–14, 15–29, and $\geq$30 km hr^{-1}). Statistical comparisons were made on mean arrival or departure times per session using a three-way ANOVA without interactions, followed by Tukey post-hoc tests. Means were considered the best estimate of central tendency for small numbers of departing birds, especially if the majority of birds left at one time and the rest left after a lapse of several minutes. We used hierarchical Type I sums of squares because weather was somewhat dependent on time of year (e.g., more cloudy days in winter), and we wished to determine the effect of date on mean arrival and departure times after the effects of cloud cover and wind had been considered. Interactions could not be included in the model because not all wind and cloud categories occurred within each date category. Tests were performed using GLMs in SPSS 8.0 (SPSS 1997). Residuals were inspected for deviations from normality and homoscedasticity. Tolerance for type I error was set at 5%. Average times that birds spent at nearshore feeding areas were calculated by adding mean arrival and departure times relative to sunrise and sunset to the median number of daylight hours during each date period. Means ± SD are given.

RESULTS

Harlequin Ducks were never seen near shore during the night. Around sunset, birds in small flocks flew or infrequently swam 1–3 km offshore, where they spent the night scattered in small groups over an area at least 1 km wide and 10 km long parallel to the shore of the Hornby Island study area. Mean sizes of departing (3.2 ± 2.5), offshore (3.7 ± 3.5), and incoming (2.8 ± 1.5) flocks were slightly, though highly significantly different due to large sample sizes ($F_{2,2675} = 22.5$, $P < 0.001$, $r^2 = 0.02$; all Tukey post-hoc tests, $P < 0.01$). The frequency of larger flocks was greater in offshore than departing groups (comparing frequencies of flocks <10 and ≥10: $\chi^2_1 = 13.5$, $P < 0.001$), and greater in departing than arriving groups ($\chi^2_1 = 12.1$, $P = 0.001$). Two was the most frequent (>50%) flock size in all cases, and 95%, 90%, and 85% of incoming, departing, and offshore flocks, respectively, were composed of five birds or less.

The earliest arrival time recorded was 32 min before sunrise on 2 November. Latest departure time was 32 min after sunset on 16 December. Feeding occurred as early as 11 min before sunrise and as late as 27 min after sunset. Offshore birds were not observed feeding during dawn or dusk, but were observed preening.

Mean arrival time did not vary significantly in relation to cloud cover or wind, but differed among date categories ($F_{2,\,17} = 3.8$, $P < 0.05$, $r^2 = 0.26$; Fig. 1). Mean arrival times per observation session averaged 12 min before sunrise, 1 min after sunrise, and 3 min before sunrise during winter, spawning, and spring, respectively (Tukey post-hoc tests were not significant). Departure times were affected by percent cloud cover ($F_{1,\,13} = 6.9$, $P < 0.03$), wind speed ($F_{2,\,13} = 5.9$, $P < 0.02$), and date ($F_{2,\,13} = 5.4$, $P < 0.02$, overall $r^2 = 0.58$). Wind direction was not important ($P > 0.5$). Departure times averaged 21 min earlier on cloudy than clear days, and 41 and 37 min earlier in winds ≥30 km hr^{-1} than in winds 0–14 (Tukey post-hoc: $P < 0.02$) and 15–29 km hr^{-1} ($P < 0.05$), respectively. Mean departure times were 1 min after sunset during both winter and spring, and 56 min before sunset during spawning ($P < 0.05$ for post-hoc comparisons between spawning and other seasons; Fig. 1).

The effects of wind and cloud cover on departure times were most pronounced during spawning. Birds left 72 min earlier on days with ≥90% cloud cover than on clearer days during spawning, compared to 12 min earlier on cloudy days in winter. The effect of wind speed was seen only during spawning. Departure times during spawning were 100 min earlier in winds ≥30 km hr^{-1} than in winds 0–14 km hr^{-1}. Average departure times showed no trends in relation to wind during other seasons. Effects of cloud cover and wind were partially confounded because strongest winds came from the southeast and tended to be associated with cloudy weather.

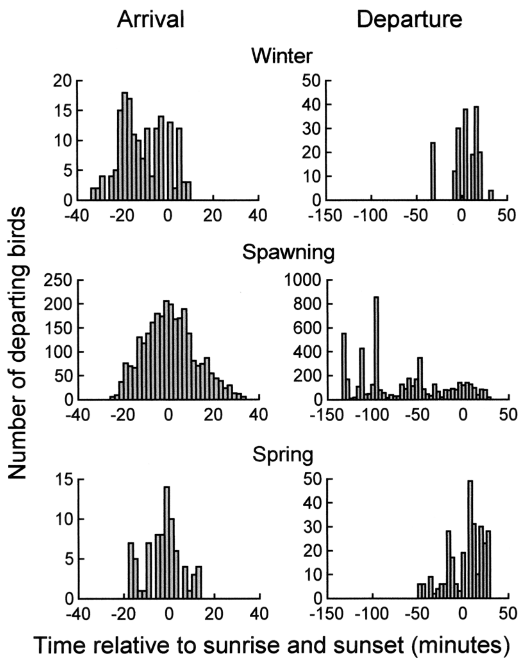

FIGURE 1. Timing of arrival and departure of Harlequin Ducks at nearshore, diurnal feeding areas on Hornby Island, British Columbia, during winter, herring spawning, and spring, 1998–2000.

Variance of arrival and departure times differed significantly by direction (arrival or departure; $F_{1,\,22} = 167.7$, $P < 0.001$), date category ($F_{2,\,22} = 124.7$, $P < 0.001$; all Tukey pairwise comparisons, $P < 0.001$), and the interaction of direction and date ($F_{2,\,22} = 80.9$, $P < 0.001$). The interaction was significant because departure times were more variable than arrival times during spawning and spring, but not during winter.

Median times spent at nearshore feeding areas were 8 hr 30 min, 11 hr 12 min, and 13 hr 48 min during winter, spawning, and spring, respectively.

DISCUSSION

Arrival and departure times of Harlequin Ducks were influenced by food availability and the associated temporal constraints on foraging time caused by limited day length. Birds extended the time available for foraging by arriving about 10 min earlier during winter. Arrival and departure times were more synchronous, and were little affected by cloud and wind during the winter, suggesting that most birds required the full daylight period to meet their daily energy requirements at that time. Greater variation in arrival and departure times during spring than winter suggests a relaxation of time constraints as day length increased.

There was no evidence of nocturnal foraging, although some individuals in winter fed near shore until almost half an hour after sunset, when it was getting quite dark. Unlike nocturnally feeding species which may compensate for increased thermoregulatory costs and decreased foraging efficiency during stormy weather by moving earlier to feeding areas (Cox and Afton 1996, Green et al. 1999), diurnal foragers may be constrained by the length of daylight, beyond which they cannot see to feed. However, it is not clear why some diurnally foraging species with diets similar to some nocturnal feeders do not also feed nocturnally (Nilsson 1970).

Birds responded to the input of abundant food during herring spawning by arriving at feeding areas near shore a few minutes later and departing almost an hour earlier than before and after spawning. More similar arrival than departure times may have been due to energy constraints of fasting through the night. Ease of meeting daily energy requirements likely contributed to the highly variable arrival and especially departure times, and the greater response to cloudy and windy weather during spawning. However, it is interesting that Harlequin Ducks did not move offshore even earlier than they did during spawning, when only 16% of their time was spent feeding (MSR, unpubl. data). This may suggest that predation risk near shore was low during daylight hours, especially during spawning, when there were large groups of birds effecting vigilance. Alternatively, digestive constraints (Guillemette 1998) may mean that birds have to spend a majority of the day at the feeding grounds, even though feeding bouts are short. The fasting period also may prove limiting if birds move offshore too early.

Arriving and departing groups were small, and birds showed little tendency to synchronize movements. Contrary to our predictions, times were least synchronous during herring spawning, when birds should have had the temporal flexibility to coordinate their movements. Offshore groups also were small and showed no tendency to coalesce into rafts. There were significantly greater proportions of larger groups in departing and offshore than in arriving flocks, but all groups were composed of less than 30 birds, and the vast majority of groups were of less than five birds.

Overall, Harlequin Ducks adjusted their activity patterns to avoid crepuscular and nocturnal periods near shore, unless constrained by food availability and the length of daylight. Whether they chose not to feed at night because predation risk near shore was high or because they could not see to feed is unknown. Some nocturnal feeding observed in other seaducks, and suspected in Harlequin Ducks elsewhere (Bengtson 1966), suggests that Harlequin Ducks may be capable of feeding after dark. Predation risk at night may be high from mammalian predators such as mink (*Mustela vison*), which were common on shore.

The methodological implications of the study for time budget analysis indicate that using time between sunrise and sunset would provide a reasonably accurate surrogate for the time available for foraging during spring, but would be less accurate during winter and spawning. Average total time that birds were near shore was 13 min longer, 57 min shorter, and 4 min longer than the time between sunrise and sunset during winter, spawning, and spring, respectively. These differences represent error rates for the three periods of −2.5%, 7.8%, and −0.5%. Birds were not observed feeding offshore, but observations of birds preening offshore reveals that studies of time budgets at shoreline feeding areas will underestimate total time spent in maintenance activities, and suggests that birds may defer some activities until night to increase the time available for foraging during the day.

A question not answered by this study was whether individuals differed in the length of time they stayed at the feeding grounds. Known pairs always departed together, and the high frequency of flocks of two birds suggests that times for paired males and females would be the same. Whether young or unpaired birds differ in the length of time they stay near shore is unknown. During herring spawning, social courtship groups of a number of males pursuing one female were often seen near shore after the majority of birds had left for the night. The time between the first and last arrivals and departures indicates that the potential for differences among birds is large and should be considered in studies comparing activity budgets among birds differing in age, sex, or pairing status.

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LITERATURE CITED

ALTMANN, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–265.

BENGTSON, S.-A. 1966. Field studies on the Harlequin Duck in Iceland. Wildfowl Trust Annual Report 17:79–94.

BROWN, P. W., AND L. H. FREDRICKSON. 1997. White-winged Scoter (*Melanitta fusca*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 274. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

COX, R. R., JR., AND A. D. AFTON. 1996. Evening flights of female Northern Pintails from a major roost site. Condor 98:810–819.

FLEISCHNER, T. L. 1983. Natural history of Harlequin Ducks wintering in northern Puget Sound. M.Sc. thesis, Western Washington University, Bellingham, WA.

FOX, A. D., A. D. GREEN, B. HUGHES, AND G. M. HILTON. 1994. Rafting as an antipredator response in wintering White-headed Ducks *Oxyura leucocephala.* Wildfowl 45:232–241.

GOCHFELD, M. 1980. Mechanisms and adaptive value of reproductive synchrony in colonial seabirds, p. 207–270. *In* J. Burger, B. L. Olla, and H. E. Winn [EDS.], Behavior of marine animals. Vol. 4. Plenum Press, New York.

GOUDIE, R. I. 1999. Behaviour of Harlequin Ducks and three species of scoters wintering in the Queen Charlotte Islands, British Columbia, p. 6–13. *In* R. I. Goudie, M. R. Petersen, and G. J. Robertson [EDS.], Behaviour and ecology of sea ducks. Canadian Wildlife Service Occasional Paper No. 100, Ottawa, Canada.

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

GREEN, A. J., A. D. FOX, B. HUGHES, AND G. M. HILTON. 1999. Time-activity budgets and site-selection of White-headed Ducks *Oxyura leucocephala* at Burdur Lake, Turkey in late winter. Bird Study 46:62–73.

GUILLEMETTE, M. 1998. The effect of time and digestion constraints in Common Eiders while feeding over blue mussel beds. Functional Ecology 12: 123–131.

GUILLEMETTE, M., R. C. YDENBERG, AND J. H. HIMMELMAN. 1992. The role of energy intake rate in prey and habitat selection of Common Eiders *Somateria mollissima* in winter: a risk-sensitive interpretation. Journal of Animal Ecology 61:599–610.

HAEGELE, C. W. 1993. Seabird predation of Pacific herring, *Clupea pallasi,* spawn in British Columbia. Canadian Field-Naturalist 107:73–82.

LIMA, S. L., AND L. M. DILL. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619–640.

MILLER, M. R. 1985. Time budgets of Northern Pintails wintering in the Sacramento Valley, California. Wildfowl 36:53–64.

NILSSON, L. 1970. Food-seeking activity of south Swedish diving ducks in the non-breeding season. Oikos 21:145–154.

PHILLIPS, J. C. 1925. A natural history of the ducks. Vol. 3. Houghton Mifflin, Boston, MA.

SPSS INC. 1997. SPSS Graduate pack 8.0 for Windows. SPSS Inc., Chicago.

US NAVY [ONLINE]. 2000. U.S. Naval Observatory astronomical applications: data services. ⟨riemann.usno.navy.mil/AA/data/⟩ (15 November 2000).