Allocating Foraging Effort Across Multiple Time Scales: Behavioral Responses to Environmental Conditions by Harlequin Ducks Wintering at Cape St. Mary's, Newfoundland

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Abstract.—Foraging behavior of Harlequin Ducks (*Histrionicus histrionicus*) and its response to changing environmental conditions during winter was investigated at Cape St. Mary's, Newfoundland. Behavioral synchrony among individuals permitted continuous observations of flocks to be conducted, sometimes over entire days. Overall foraging effort of Harlequin Ducks was examined at two organizational levels: dive cycles (dive and surface pause) and foraging cycles (foraging bout and rest bout). Overall foraging effort decreased at greater tide depths as Harlequin Ducks decreased the duration of foraging bouts. Dive:pause ratios did not change within these shorter foraging bouts at high tides, however the duration of dives, pauses, and the total dive cycle all increased. Overall foraging effort decreased in response to increased wind/wave exposure due to a decrease in dive duration. Overall foraging effort did not change in response to decreasing ambient temperature; however the frequency of dive cycles decreased which could decrease energy expenditure associated with post-dive thermoregulatory costs. Overall foraging effort increased throughout the day, particularly in the last foraging bout before the overnight fasting period. Interestingly, this strategy was accomplished by decreasing dive durations but increasing foraging bout duration. These opposite results across levels of behavioral organization are interpreted in the context of intermittent exercise and locomotion whereby decreasing effort at one level of energy expenditure could allow for increased effort at another. Therefore, different (and sometimes opposite) responses to environmental conditions can occur at different levels of behavioral organization. Even when overall foraging effort remains unchanged, the strategy employed can differ in its temporal allocation or frequency, which could be important in balancing energy budgets under increased energetic costs and/or time constraints. These results have particularly important implications for interpreting behavioral responses investigated at only a single level of behavior, extrapolating data from brief observation periods to longer time scales, and foraging models which only consider single levels of behavior such as the dive cycle.

Key words.—dive cycles, foraging, Harlequin Duck, *Histrionicus histrionicus*, winter.

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Animals must make many types of foraging decisions, including prey and habitat selection and time budget allocation, in order to obtain the highest net energy gains (Pulliam 1976; Pyke *et al.* 1977; Caraco 1980). Harlequin Ducks (*Histrionicus histrionicus*) winter in a complex marine environment where these foraging decisions can be influenced by a complex suite of changing environmental conditions. Further, owing to small body size, it has been suggested that Harlequin Ducks wintering in the North Atlantic may be pushed to their physiological limits in order to survive (Goudie and Ankey 1986). Weather and oceanographic conditions in the Northwest Atlantic are severe during mid-winter, so energy requirements are expected to be high to offset associated thermoregulatory costs (Guillemette *et al.* 1992).

Animals have several options to deal with high energy demands. Increasing energy consumption by increasing foraging effort is an obvious way. For physiological reasons, resting bouts and pausing between dives are obligatory aspects of foraging for air breathing organisms (MacArthur 1986; Ydenberg and Guillemette 1991; Guillemette *et al.* 1992), and may also provide time to process and digest food (Guillemette *et al.* 1992). Therefore, individuals are probably only able to adjust foraging effort within certain limits, especially on short days during winter

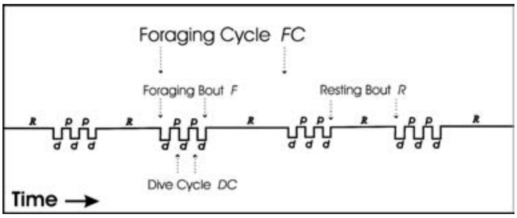

Figure 1. Schematic representation of the different components of a foraging cycle (*FC*). Dive cycles (*DC*) include a foraging dive (*d*) and subsequent surface pause (*p*). Foraging bouts (*F*) include a sequence of dive cycles, and a foraging cycle includes a foraging bout and the subsequent rest bout (*R*).

when thermal stress is greatest. This may be particularly true for wintering sea ducks, as they spend a large proportion of the day foraging (Goudie and Ankney 1986; Goudie 1999; Systad *et al.* 2000; Torres *et al.* 2002).

Some marine birds have flexible time budgets and can increase foraging intensity or reduce resting periods (Burger and Piatt 1990; Monaghan *et al.* 1994). Although surface pausing and resting bouts are obligatory aspects of foraging, few have examined how individuals can increase foraging efficiency during these periods. For example, net energy budgets could be maximized by coordinating foraging and resting bouts with certain environmental conditions. Therefore, in contrast to classical time-budget studies that examine the proportion of time spent in each activity per day, both the duration and temporal location of each type of behavior in relation to environmental conditions could play critical roles in balancing energy budgets.

In this study the foraging behavior of Harlequin Ducks under different environmental conditions (weather, tide, time of day and day length) during winter at Cape St. Mary's, Newfoundland was considered. How environmental conditions influenced temporal aspects of foraging behavior and the interrelationships of foraging behaviors across temporal scales within a day was also examined.

Temporal Organization of Behavior

Despite logistical and sampling issues (Baldassare *et al.* 1988), time-activity budgets have proven useful in determining the amount or proportion of time spent foraging per day (Goudie and Ankney 1986; Paulus 1988; Systad *et al.* 2000). However, time-activity budgets only provide an average estimate of the time spent in foraging or resting bouts, necessarily excluding variation in effort that may occur at shorter temporal and behavioral scales. A behavioral scale can be defined as the various levels in a hierarchy of behavioral categories (e.g., Fig. 1). Behavioral scales, like behavior, are dynamic (do not occur at fixed time intervals) and are determined by the organization of behavioral patterns of the species. Further, time activity budgets often extrapolate events from short term behavioral watches to longer temporal and behavioral scales. As different physiological and environmental constraints and conditions act at different time scales, the extrapolation of short-term behavior to longer time scales may not be an appropriate analytical approach. Time-activity budgets may be adequate for research on a species' general behavior, but are of too low a resolution for in-depth studies of foraging strategies.

An alternative analytical technique used for diving birds focuses on a finer behavioral scale, such as the relationship between diving and pausing on the surface (the dive:pause ratio; Dewar 1924). Recently researchers have considered that diving and pausing may be altered to change foraging intensity throughout a foraging bout. For example, dive duration could affect the subsequent surface pause (Wilson and Wilson 1988) or be influenced by dive depth and travel time to the bottom (Houston and Carbone 1992; Lovvorn and Gillingham 1996). This approach has proven effective in considerations of trade-offs between diving and recovery when diving becomes anaerobic (Ydenberg and Clarke 1989). However, empirical data are often limited to observations of sequential dive cycles over only brief periods. Each method (time-activity budgets and dive:pause ratios) alone only investigates a single temporal scale of foraging behavior, making it difficult to draw inferences across time periods, particularly when an animal forages at different rates over a foraging bout (Swennen *et al.* 1989).

For many sea ducks, the diurnal period consists of sequential foraging cycles. The various behavior patterns that can occur within a given foraging cycle (FC) are outlined in Fig. 1. A dive cycle (DC) consists of a dive (d) and the subsequent surface pause (p). Effort can be modified by increasing the duration of either the dive or pause, with or without changing the overall length of the dive cycle. A foraging bout (F) includes a sequence of dive cycles, of which the total number of dive cycles or time spent foraging varies. A foraging cycle includes a foraging bout and the subsequent rest bout (R), each of which can vary in duration. In many species the active period of the day is made up of sequential foraging cycles. Non-foraging behavior such as courtship can, for present purposes, be included in rest bouts.

A diving bird can modify foraging effort through various combinations of behavioral strategies, including modification of the duration of dives and pauses, foraging and rest bouts, and the total length of a foraging cycle. A practical example is deferring physiological recovery from diving to the subsequent rest bout rather than in surface pauses between dives (Ydenberg 1988; Ydenberg and Clarke 1989). Each behavioral component (Fig. 1: d, p, F, R) represents a different tactic that together make up a behavioral strategy. Although numerous combinations of the frequency and duration of these behavioral tactics are possible, only those yielding foraging strategies that increase long term net energy gain over various environmental, ecological and physiological constraints will be favored by natural selection (Schoener 1971). The present paper therefore explores how Harlequin Ducks allocate foraging effort at (a) the level of dive cycles, (b) foraging cycles, and (c) cumulatively across dive and foraging cycles (overall foraging effort), in relation to various environmental constraints.

Methods

Harlequin Ducks foraging at Cape St. Mary's, Newfoundland in Jan-Apr and Nov 2000 were observed through more than 2,500 dive cycles and 100 foraging cycles. The local population consists of approximately 100 individuals that almost exclusively use a few foraging patches within five to six km (JPH and T. Power unpub. data). Overcoming the constraints of time-activity budgets and dive pause techniques to examine interactions among behavioral scales requires continuous observations, be it through revised observational techniques, or through animal-bourn time activity loggers or telemetry. Activities of individual Harlequin Ducks at Cape St. Mary's were extremely coordinated within flocks (see also Schenkeveld and Ydenberg 1985). This highly coordinated activity meant the duration of any behavior was the same for all individuals in a flock; these circumstances therefore allowed us to use a flock, instead of the individual, as the unit of study. Observations on entire flocks from the arrival of birds at dawn, until the birds flew several km offshore for the night, were attempted. Flock size varied throughout the day ($\bar{x}$ = 20 individuals, range = 3 - 44). When flocks split into smaller groupings, the largest grouping was observed. Often, soon after a flock had fragmented, the individuals would join to reform the original flock. In some situations when diving became less synchronous, continuous observations were maintained by selecting the largest observable sub-group (sub groups still maintained synchrony despite asynchrony with the entire flock). In this manner, a large proportion of the population could be simultaneously observed and followed throughout sequential foraging cycles, and sometimes throughout an entire day. The variables measured included dive and surface pause durations, duration of foraging bouts, subsequent rest bouts, and foraging cycles (Fig. 1). In the calculation of group dive and pause durations it was assumed that the first sub group of individuals to dive were the first to surface. Group dive and pause durations were obtained by averaging over sub groups. Observations of identifiable individuals indicated that these assumptions held 94% of the time (N = 112 dives and pauses; the remaining 6% affected calculations by only one s or less). Pause durations significantly increased when flocks of foraging Harlequin Ducks joined (t_{2733} = 14.6, $P < 0.0001$) or when large waves forced Harlequin Ducks to dive into them, but not descend (t_{2653} = 6.4, $P < 0.0001$), so these data were excluded from analyses relating pause behavior with other environmental variables.

Weather data (wind speed, km/h, and temperature, °K), were obtained from the Argentia, Newfoundland weather station records. Tide depth data were obtained from tide tables, and categorically ranked from low (0) to peak (6) or intermediate (1-5) by dividing the total tidal height difference (high tide amplitude – low tide amplitude) into seven equal categories.

Linear regression and analyses of variance were used to evaluate relationships between foraging behavior and environmental conditions. The focus of analysis is on main effects to illustrate interactions among temporal scales of behavior. Interactions among foraging behaviors were explored using correlation analysis.

RESULTS

Summary statistics of dive behavior across all environmental conditions are presented in Table 1.

Table 1. Mean plus or minus standard error and sample size (N) of Dive, Pause, Foraging Bout and Resting Bout durations (s), and dive:pause and foraging:resting bout ratios, summarized across all environmental conditions.

Behavior	Mean ± SE (s)	N
Dive	18.3 ± 0.1	2,841
Pause	19.3 ± 0.2	2,739
Dive:Pause	1.157 ± 0.013	2,738
Foraging Bout	1,142 ± 84	116
Resting Bout	1,224 ± 101	110
Foraging:Resting	1.637 ± 0.227	109

Environmental Conditions

With increasing wind speeds dive duration declined, no other relationship was significant (Table 2). At warmer air temperatures, dive, pause and dive cycle durations significantly decreased, while there was no significant relationship with any foraging cycle variable and air temperature (Table 2). Dive duration, pause duration and dive-cycle duration were positively related to tidal depth, while foraging bout duration and the F:R ratio declined significantly with tidal depth (Table 2, Fig. 2). Throughout the day, dive durations and dive:pause ratios decreased, while foraging bout durations and F:R ratios increased significantly as the day progressed (Table 2). With increasing day length, dive durations and dive:pause ratios increased, as did resting bouts and foraging cycles (Table 2).

Relationships Among Behaviors

Across all environmental conditions combined, dive duration was correlated with the duration of the subsequent pause (r_{2532} = 0.646, $P < 0.0001$). Dive duration was also related to the duration of the previous pause, though this relationship did not account for as much variation (r_{2579} = 0.216, $P < 0.0001$). Foraging bout duration was not related to the duration of the subsequent rest bout (r_{89} = -0.02, n.s.) or of the previous rest bout (r_{78} = -0.122, n.s.). Dive:pause ratios were negatively related to the durations of dive cycles (r_{2532} = -0.212, $P < 0.0001$). Longer dive, pause and dive cycles were associated with longer foraging bout and shorter resting bouts (Table 3).

Across all environmental conditions considered together, dive duration ($F_{1, 3345}$ = 3.3, n.s.) and dive cycle duration ($F_{1, 3203}$ = 1.1, n.s.) were not related to position within foraging bouts. As time remaining in the foraging bout decreased, pause durations significantly increased ($F_{1, 3211}$ = 3.85, $P = 0.05$) while dive:pause ratios significantly decreased ($F_{1, 3203}$ = 11.0, $P = 0.0009$).

DISCUSSION

Weather

Although the same total amount of time is spent underwater in foraging cycles at all ambient air temperatures, dive bouts were longer and less frequent at colder temperatures. We expected increased foraging effort under colder temperatures, but it is possible that Harlequin Ducks could increase net energy gain during colder temperatures through longer but fewer dive cycles, with-

Table 2. Relationship between environmental conditions and Harlequin Duck foraging behaviour at Cape St. Mary's, Newfoundland. Significant results and slope of direction indicated by +/- (P > 0.05) or ++/-- (P > 0.001), n.s. is not significant.

	Dive cycle (DC)				Foraging cycle (FC)			
	Dive	Pause	Dive cycle duration	Dive:pause ratio	Foraging bout	Rest bout	Foraging cycle	Foraging:rest ratio
Wind/wave exposure	—	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Temperature	—	—	—	n.s.	n.s.	n.s.	n.s.	n.s.
Tide	++	++	++	n.s.	—	n.s.	n.s.	—
Time of day	—	—	n.s.	n.s.	+	n.s.	n.s.	+
Day length	+	n.s.	n.s.	+	n.s.	++	++	n.s.

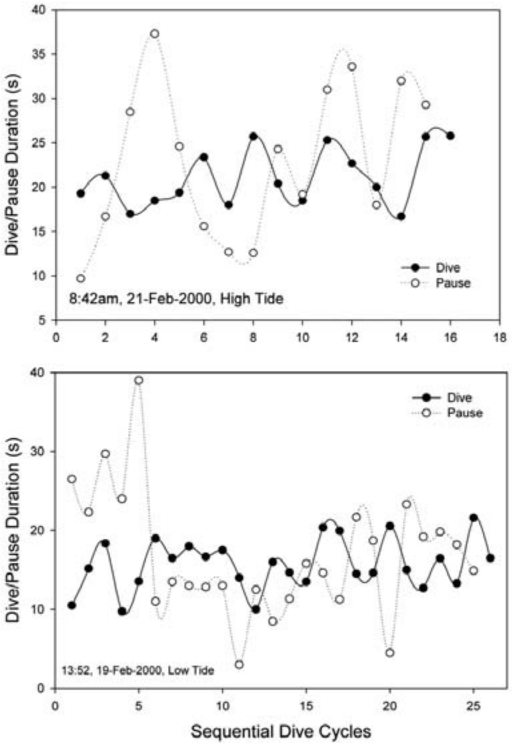

Figure 2. Fluctuation of the dive and pause durations over sequential dive cycles within two foraging bouts. Spline-smoothed in Sigma Plot 2000.

out increasing total dive time. For example, air trapped in plumage is released upon buoyant ascent by Long-tailed Ducks (*Clangula hyemalis*) and Common Eiders (*Somateria mollissima*) (JPH unpublished data), and diving animals typically decrease body temperature when submerged (Bevan and Butler 1992). Less frequent/fewer dives could therefore reduce energy costs of warming air within plumage air spaces and raising body temperature after each dive. In this manner, Harlequin Ducks could spend the same amount of time foraging but decrease energy expenditure by changing the temporal allocation of foraging effort. In Newfoundland and Alaska (Goudie and Ankney 1986; Fischer and Griffin 2000) has found that wintering Harlequin Ducks spent greater proportions of the day feeding when temperatures were colder even when day length was accounted for, though this relationship was not reported in British Columbia (Goudie 1999) where waters and air are considerably warmer. In contrast, we found that temperature did not influence overall foraging effort, only how it was temporally allocated.

Dive durations decreased in relation to increasing wind speed while no other foraging activities were affected, indicating that total foraging effort decreased with increasing wind speed, and associated increases in wave exposure. This finding was contrary to our expectation that increased thermoregulatory demands (due to increased convective heat loss from both turbulent air and water) would lead to increased foraging effort. It is possible that shorter dive durations were beneficial due to increased wind induced wave exposure in the inter-tidal foraging zone of Harlequin Ducks, which could affect both prey distribution and increase diving costs due to strong local water currents. Other behavior during surface pauses and resting bouts, such as preening and resting, could also have been influenced by weather in order to offset thermoregulatory costs (Brodsky and Weatherhead 1985). No relationship between wind speed and proportion of time spent foraging has been reported in other studies of Harlequin Ducks (Goudie and Ankney 1986; Goudie 1999).

Table 3. Correlation analyses between dive cycle and foraging cycle time scales of behavior, combined across all environmental conditions. Degrees of freedom ranged from 107-114, * denotes P > 0.05.

	Foraging	Resting	Foraging Cycle	Foraging:Rest
Dive	0.22*	-0.20*	-0.04	0.21*
Pause	0.21*	-0.26*	-0.08	0.21*
Dive cycle	0.24*	-0.25*	-0.06	0.23*
Dive:pause	-0.01	0.196*	0.156	-0.05

Tide

As expected, dives were longer when waters were deep during high tides. Pause and total dive cycle durations were also longer, and accordingly dive:pause ratios did not differ over tidal depths. Increased dive duration could be due to increased travel times at greater water depths. Pauses likely increased to allow recovery from longer dives, leading to a decrease in the frequency of dive cycles but not to a change in the proportion of time underwater. In contrast, the duration of foraging bouts decreased with increasing tidal depth, with no change in rest bout duration. Although dive cycle duration increased with tidal depth, overall foraging effort decreased as foraging bout duration (and therefore total number of dive cycles) decreased. Therefore, overall foraging effort was greater during lower tides, despite shorter dive durations during these periods. Interestingly, tidal height was positively related to time spent feeding in Alaska (Fischer and Griffin 2000) and negatively related to time spent foraging in British Columbia (Goudie 1999). These differences likely arise from the amount and distribution of intertidal habitat and potential movement by prey of Harlequin Ducks in these areas, which may become available at different tides at different sites. Alternatively, as our results were different across two behavioral scales, conflicting results of other research could be a function of sampling methods and subsequent calculations based on scaling shorter behavioral watches to longer term foraging indices.

Time of Day

Total foraging effort increased throughout the day as increases in foraging bout duration (particularly for the last foraging bout of the day in mid-winter) were much greater than the total decreases in effort due to shorter dive durations. Shorter dive durations (with no change in pause duration) may be required to maintain foraging effort over long foraging bouts. Diving and pausing, and foraging and resting bouts, can both be considered levels of intermittent exercise, and therefore a decreased rate of foraging (e.g., more frequent pausing) could reduce fatigue allowing endurance required to conduct longer foraging bouts (Wienstein 2001). The last foraging bout of the day in mid-winter was often much longer than other foraging bouts. Physiological recovery and digestive processing from the longer foraging bout could be deferred to the overnight fasting period, and the increased energy could be important for overnight survival or maintenance of body condition. Flocks often flew or drifted offshore directly following the final foraging bout. Other studies have shown an increase the proportion of time spent feeding as the day progresses (Goudie and Ankney 1986; Fischer and Griffin 2000; Mittelhauser *et al.* 2008). Our results show that this increase is due to an increase in foraging effort, but apparently requires a reduction in dive duration. This is an important finding, as behavioral response to an environmental condition differed in opposite directions across two linked levels of behavior.

Day Length

Dive but not pause durations were longer, while resting-bout duration increased with no increase in foraging-bout duration, over longer days. This is similar to findings of other research on Harlequin Ducks (Goudie and Ankney 1986; Fischer and Griffin 2000; Mittelhauser *et al.* 2008) that report an increase in the proportion of time spent foraging on short days. However, when considering total hours spent foraging (extrapolated from short behavioral watches), Harlequin Ducks increased the amount of absolute time spent foraging as the winter progressed and days became longer (Fischer and Griffin 2000; Torres *et al.* 2002), likely as a function of being able to include more foraging cycles in a day, even if the resting bouts between them were longer.

Relationships Among Behaviors

Inter-relationships among behaviors may be related to physiological and endurance considerations associated with expending energy. Although this is an area rarely addressed in the foraging literature, the frequency of energy expenditure at short time scales can be important in determining endurance over longer time scales (Kramer and McLaughlin 2001; Wienstein 2001). This can be important in maximizing net energy gain if the work being conducted is foraging (Williams *et al.* 2000).

Within foraging bouts, pause durations increased as the foraging bout progressed, although dive durations did not change. These longer pauses could be important in reducing fatigue effects accumulated over a foraging bout. Interestingly, a visual inspection of the specific organization of dive cycles within individual foraging bouts indicates that foraging effort (e.g., dive:pause ratio) periodically cycles throughout the bout (Fig. 2). Such cyclicity in effort expenditure could be important in many ways, such as increasing endurance, but has also been suggested to include potential cognitive and perceptual benefits allowing a forager to more effectively exploit its resources (Wienstein 2001).

As has often been found for diving birds, pause duration was related to the duration of preceding dives, in concordance with hypotheses regarding pauses being a function of aerobic recovery from diving (Ydenberg 1988; Houston and Carbone 1992). However, dive-pause relationships have primarily been addressed in the context of high rates of work by theoretically maximizing foraging rate and empirically excluding long pauses from analyses. As aerobic recovery may occur fairly quickly (Halsey *et al.* 2003), the dive:pause relationship may not be as strong for longer dive durations (e.g., Goudie 1999). Pause durations are also likely a function of digestive constraints (Guillemette 1994, 1998; though this may be less important for Harlequin Ducks given more easily digestible prey) and benefits of intermittent locomotion and recovery from fatigue during extended periods of work. Additionally, although dive and pause length co-varied positively under given tidal and weather conditions, they were differentially affected over time within foraging bouts, time of day, and time of year. This indicates the dive-pause relationship is plastic and can be an important behavioral tactic with which diving birds can modify foraging effort.

Longer dives, pauses and dive cycles were related to increasing foraging bout durations, decreasing resting bout durations, and increasing F:R ratios, and therefore increasing foraging effort at the scale of foraging cycles. Therefore, within foraging cycles with higher foraging effort, the frequency of dive cycles, but not necessarily overall dive cycle effort (e.g., dive:pause ratio) decreases. Although this trend was observed across all environmental conditions combined, it is important to note that the analysis of tidal depths (longer dive cycles within shorter foraging bouts) and time of year (longer dives, greater dive:pause ratios within longer foraging cycles with longer rest bouts) indicated foraging effort can increase at the scale of the dive cycle with decreasing effort at the foraging cycle scale under some conditions. How Harlequin Ducks utilize this tradeoff could depend on the environmental and physiological conditions and the effects of these conditions on energetics, which could differ among behaviors and across behavioral scales. For example, factors such as tide that affect behavior at the scale of individual dives, compared to factors such as ambient air temperature, which influence Harlequin Ducks during surface pauses and resting bouts, could lead to different allocation of foraging effort. Across environmental conditions, rest bout duration was related to dive cycle effort in the previous foraging bout, indicating that foraging bouts with high effort required longer post-rest bouts. This finding is consistent with tradeoffs in effort expenditure among scales, and with the suggestion of Ydenberg and Forbes (1998) that in some situations physiological recovery from diving could be deferred to resting bouts.

Foraging and subsequent resting bout durations were not related. Although digestion and recovery from extended period of exercise could set a minimum limit on resting bouts as a function of foraging bouts, the foraging:rest bout relationship could be more plastic than dive:pause relationships, and could provide a useful behavioral tactic for Harlequin Ducks to adjust foraging effort. The dependence of pause duration on dive duration may only hold under high rates of foraging where pause duration approaches the minimum aerobic recovery period. This circumstance could also hold at the scale of the foraging cycle when rest bout durations approach minimum physiological recovery time from exercise. We explored this idea by analyzing only shorter foraging and resting bouts (i.e. F < 3,000 s; R < 1,250 s), and found that under these circumstances, rest bout duration was significantly and positively related to preceding foraging bout duration ($F_{1, 64} = 10.3$, $P = 0.002$).

Sequential Behavior

Sequential behaviors have often been ignored in animal behavior due to stringent sampling regimes attempting to remove biases of autocorrelation and independence of data points in statistical analysis. However, the interdependence of behavioral processes is biologically and ecologically interesting and clearly represents important ways in which individuals respond to environmental variation. Sequential data on foraging by diving birds is practically absent in the literature (but see Ydenberg and Forbes 1988; Ydenberg and Guillemette 1991). Given the unique continuous data we were able to collect, we present a series of examples illustrating sequences of foraging behavior by Harlequin Ducks.

Fig. 3 illustrates sequential dive cycles within two foraging bouts. Similar to Ydenberg and Guillemette (1991) effort seems to vary cyclically. Although we cannot explain all of the variation occurring between dive cycles, there are several potential explanations. Variation in effort may reflects responses of Harlequin Ducks to patch scale fluctuations in the availability of amphipods (their primary prey) and the ability of Harle-

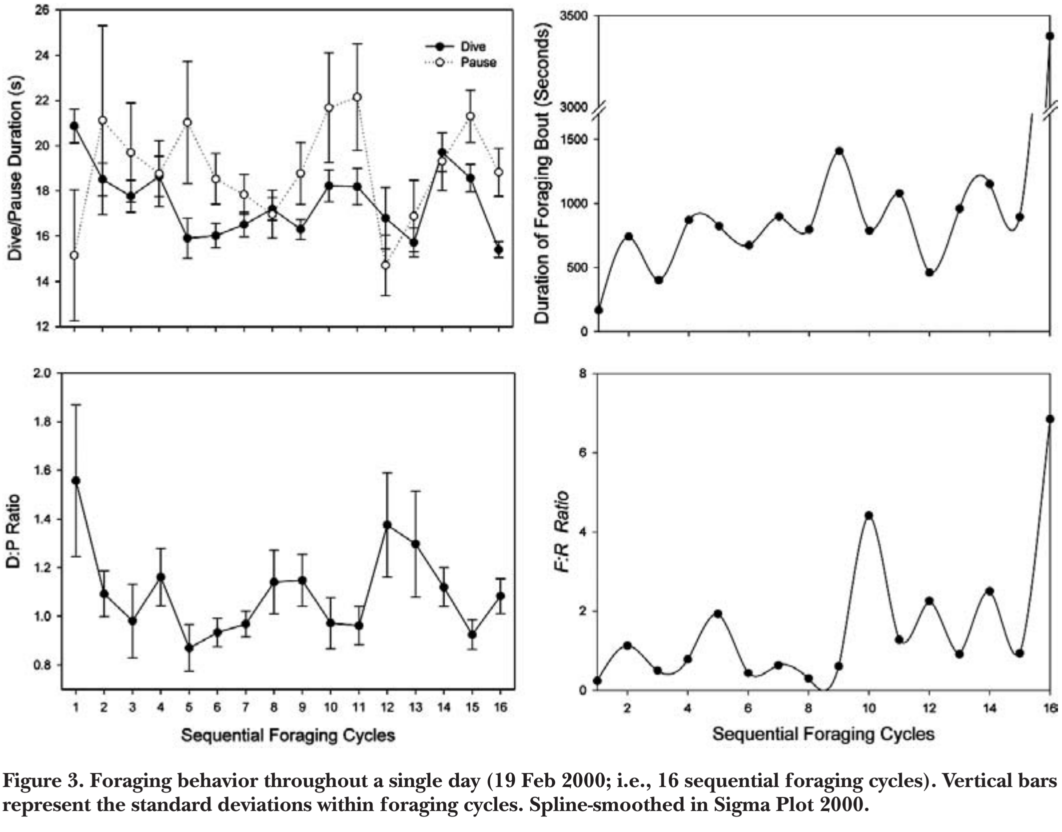

Figure 3. Foraging behavior throughout a single day (19 Feb 2000; i.e., 16 sequential foraging cycles). Vertical bars represent the standard deviations within foraging cycles. Spline-smoothed in Sigma Plot 2000.

quin Ducks to track prey dispersion in patch selection. Assuming relatively unchanging average prey density, this cyclicity could be due to the benefits of intermittent exercise and locomotion. Intermittent and cyclic effort of Harlequin Ducks could provide a tactic that allows them to a) make more effective foraging decisions by pausing to evaluate options with changing circumstances and b) exert high rates of foraging interspersed by less rigorous foraging that could allow partial avoidance of fatigue effects and allow maintaining higher average foraging effort over longer periods (Kramer and Mclaughlin 2001; Wienstein 2001).

Fig. 3 illustrates variation in effort throughout a day at the scales of the dive cycle and of the foraging cycle. Effort also appears to be cyclical at these behavioral scales, above and beyond that explained by tidal cycle variation. The increase in foraging effort that often occurs within the last foraging cycle of the day preceding the overnight fasting period is clear (Fig. 3). Interestingly, the first foraging bout of the day was often fairly short, although at least in this example, dive:pause effort this was much higher within that bout.

CONCLUSIONS

This study investigated only two levels of behavioral organization. Finer time scale behaviors, such as travelling, searching, and prey consumption that occur within individual dives, and coarse scales such as diurnal activity and maximizing fat stores over winter, must be important in influencing behavioral decisions and activity allocation across time scales. Such influences therefore may have played a role in the results at the time scales investigated in this study. Our results clearly emphasize that the interdependence of behavioral decisions represents an important and fascinating area of animal behavior that has yet to be fully explored. Decisions at one time will be influenced by those at others, particularly when decisions occur over hierarchical categories. The temporal scale chosen over which to sample behavior will be critical, and behavior quantified at short intervals might not be accurately extrapolated to longer time scales, as is often done. The results of analysis can change, sometimes in opposite directions, depending on the behavioral/temporal scale considered. As illustrated in the present study, this can have important implications for understanding and interpreting the foraging behavior of diving birds and undoubtedly other mobile predators as well.

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