

DIVING BEHAVIOR IN SURF SCOTERS AND BARROW'S GOLDENEYES

GUY BEAUCHAMP¹

*Behavioural Ecology Research Group, Department of Biological Sciences,
Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada*

ABSTRACT.—I investigated diving behavior in foraging flocks of wintering Surf Scoters (*Melanitta perspicillata*) and Barrow's Goldeneyes (*Bucephala islandica*). Individuals in flocks of scoters and goldeneyes tended to dive and surface in a highly synchronous fashion. Diving-party size explained a large amount of variation in observed levels of diving synchrony. Synchrony increased with flock size as individuals in large groups followed one another more quickly during foraging dives than birds in smaller parties. Synchrony may be advantageous in large groups to maintain cohesion during foraging trips. Scoters and goldeneyes appeared not to adjust diving behavior in the presence of kleptoparasitic Glaucous-winged Gulls (*Larus glaucescens*). The length of the pause between consecutive dives was positively correlated with the duration of the preceding dive in the two species. Based on these relationships, the deviation from the estimated surface time was obtained for each series of dives. In both species, pause duration in sequences of many dives tended to oscillate around predicted values. This supports the idea that divers foraging on sessile prey complete more of the recovery after each dive than birds foraging on mobile prey who occasionally delay repayment of the physiological debt. Received 13 September 1991, accepted 22 February 1992.

IN A NUMBER of bird species, search for food occurs underwater. A typical dive cycle in these birds includes underwater time, during which individuals travel to the foraging area, search for food, and return to the surface, and surface time between successive foraging episodes. Pauses between dives may be used by the birds to recover from the physiological effects of a prolonged period of time spent underwater. A great deal of research has focused on the physiology of diving (e.g. Butler and Jones 1982), but comparatively little attention has been paid to the behavioral ecology of diving in birds. Two aspects of diving behavior in birds have, however, received increased attention recently: synchronicity; and the relationship between dive and pause duration.

In flocks of diving birds, submersion schedules are often temporally clustered. Individuals in groups of birds thus tend to dive and surface in synchrony (McKinney 1965, Stewart 1967, Schenkeveld and Ydenberg 1985, Wilson et al. 1986). In the particular case of birds foraging on sessile prey, synchrony may allow individuals to follow one another to extremely localized food patches (McKinney 1965). In addition,

Schenkeveld and Ydenberg (1985) suggested the possibility that individuals in these flocks gain protection while surfacing with a prey by swamping potential kleptoparasites. In a quantitative study of diving by Surf Scoter (*Melanitta perspicillata*) flocks, Schenkeveld and Ydenberg (1985) provided evidence that diving and surfacing are highly synchronous in this species. Surfacing synchrony also tended to increase in the presence of Glaucous-winged Gulls (*Larus glaucescens*) that commonly rob mussels from scoters. Little is known about other factors that lead to large variation in the degree of synchrony exhibited by different flocks.

Diving birds also show flexibility in the control of dive duration. Data from a variety of species indicate that pause duration is generally positively related to the amount of time spent underwater in the preceding dive (see review in Ydenberg 1988). This supports the assumption that pause duration is linked to recovery from the physiological effects of diving. However, recent evidence also suggests that surface time in a series of dives may be altered to suit local foraging conditions. For instance, Western Grebes (*Aechmophorus occidentalis*) can delay repayment of the accumulated physiological debt until after an encountered school of fish escapes (Ydenberg and Forbes 1988). Shorter pause duration than would be needed for full recovery may allow a forager to relocate and exploit more

¹ Present address: Department of Biology, Concordia University, 1455 Ouest Boulevard de Maisonneuve, Montréal, Québec H3G 1M8, Canada.

efficiently transient schools of fish. In contrast, the tendency to delay recovery in this fashion was found to be reduced, but not absent, in Common Eiders (*Somateria mollissima*), a large sea duck that forages on sessile or slowly moving prey (Ydenberg and Guillemette 1991). More evidence is needed to understand why divers exploiting sessile prey do not complete more of the physiological recovery after each dive.

In this paper, I investigate diving behavior by flocks of Surf Scoters and Barrow's Goldeneyes (*Bucephala islandica*). Surf Scoters and Barrow's Goldeneyes winter in large numbers in southern coastal British Columbia, Canada. The two species forage by diving in apparently synchronous fashion and feed primarily on sessile mussels (*Mytilus edulis*). Here, I examine potential sources of variation in the level of synchrony exhibited by diving flocks and relate pause duration to dive time spent underwater in two species, where the tendency to delay recovery after each dive should be reduced.

METHODS

I studied flocks of Surf Scoters and Barrow's Goldeneyes in Stanley Park, Vancouver, British Columbia, between 4 December 1990 and 25 February 1991. A large population of these birds winter in Stanley Park and individuals gather in flocks ranging in size from 3 to over 100. Foraging flocks of the two species dove for mussels attached to rocks along the seawall, from which observation on diving behavior could be made at close range.

Male Barrow's Goldeneyes reunite with their mate on the wintering area, and some pairs are known to defend territories along shorelines (Savard and Smith 1987). In Stanley Park, territorial birds often chased away flocks of Surf Scoters diving nearby. Nevertheless, individuals in flocks did not display any obvious aggressive behavior. Casual observation showed that the territorial, paired birds often joined larger flocks of goldeneyes. Most paired birds in the study area showed no territoriality and joined flocks of various sizes. Multispecies flocks, in which goldeneyes joined Surf Scoters, were seen frequently.

I collected data by patrolling the seawall during the high-tide period until a foraging flock of scoters or goldeneyes within camera range (<50 m) was encountered. A videotape of the diving flock was made. In the following, flock size refers to the number of individuals in a diving party. Not all individuals in a group joined the diving party, and they most often remained on the edge of the flock for the entire recording sequence. Flock sizes reported below do not include these individuals since it is the duration of the interval between successive individual dives that is used to define synchrony. On many occasions, a diving party was joined by newly arrived individuals,

or, conversely, members of the diving party left the group during a pause on the surface. Recording stopped when flock size changed by more than two during the diving sequence. Hence, it was possible to analyze synchrony in flocks of known and stable sizes. Any particular flock was only monitored once on a given day.

In a typical recording, a flock of scoters or goldeneyes would approach the seawall and start diving for mussels. One bird would begin to dive, to be followed by individuals nearby. The submersion wave would then propagate throughout the flock. Individuals remained underwater on average for about one-half minute and surfaced in a similarly organized fashion. Dives were then followed by a pause of similar duration during which birds moved away from the seawall and handled mussels brought back to the surface. Individuals surfaced most often with single mussels but also brought back small clumps of prey that required considerable handling before being swallowed whole. After spending some time on the surface, scoters and goldeneyes would approach the seawall again for a new dive cycle. Diving behavior by a particular flock was monitored until five or six dive cycles had been recorded. However, on a number of occasions recording stopped before the limit because flocks were disturbed by the presence of passersby. Commonly, a large flock would break down into smaller parties or individuals would simply leave the area.

Measuring synchrony.—The video sequences were analyzed on a video monitor. Diving events were keyed on an event recorder to an accuracy of 1 s. I used the technique developed by Schenkeveld and Ydenberg (1985) to measure diving and surfacing synchrony in scoter and goldeneye flocks. The method is based on a comparison of the distribution of intervals between successive departures from (or arrivals to) the surface by individuals in a given flock with the negative exponential distribution that is expected if birds behaved independently of one another. Synchronous diving or surfacing would produce more short and fewer long intervals than expected from the null hypothesis. For each flock tested, I pooled interdive (or intersurfacing) intervals from the whole sequence of many successive dive cycles. In doing so, one must be able to define clearly the beginning and end of a particular dive by the group in the sequence. Practically, one dive for a given flock began at the first submersion and ended when one bird from the group surfaced. Diving events were keyed during this particular time window. Surfacing events were then keyed as the first few birds surfaced. This process was repeated for the whole sequence of dive cycles after which diving and surfacing events were pooled to get an overall measure of synchrony for the flock.

Typically, all birds in a flock of size n quickly submerged and reappeared on the surface together. The number of birds on the surface, therefore, was n when individuals paused or 0 when foraging occurred. However, in some flocks the rhythm of diving events

broke down. For instance, birds would often submerge while some individuals were still underwater. As a consequence, the number of birds on the surface was always greater than 0 and smaller than n . In such a case, it is difficult to identify the beginning and end of one particular dive for the group. I excluded from the analysis all flocks for which it was impossible to identify clearly the beginning and end of a dive in a sequence of successive dive cycles. Overall, nearly 10% of all sequences fitted in this category. Sequences of this nature involved primarily small flocks that foraged in very shallow waters (<1 m).

I also excluded from the analysis all flocks with sizes larger than 60, because diving and surfacing occurred so rapidly in these flocks that I could not key events quickly enough on the event recorder while watching the monitor screen. Multispecies flocks also were excluded from the analysis, because goldeneyes and scoters tended to segregate in these flocks and seemingly followed only members of their own species while diving. Typically, goldeneyes would be found at the forefront of a diving party and would complete two or three dive cycles, while scoters were still underwater. Measuring synchrony and dive duration for the entire multispecies flock is therefore problematic.

Distributions of interdive (or intersurfacing) intervals were tested for clumping by using the Anderson-Darling statistic (A^2 , Stephens 1974). This goodness-of-fit statistic uses no arbitrary classification of data into categories and is based on a ranking of the standard exponential variates of the observed intervals. In general, the Anderson-Darling statistic provides a more powerful test of the null hypothesis than the chi-square technique on discrete data. In the following, the exact value of this statistic also is used as an index of diving and surfacing synchrony. Large values of the index define highly synchronous events.

Effects of the presence of gulls on synchrony.—Glaucous-winged Gulls are known to steal food from scoters and goldeneyes by attacking them as they surface with mussels (e.g. Schenkeveld and Ydenberg 1985). Along with flock size, I recorded the number of gulls that closely attended any particular group under scrutiny. Overall, one or more gulls attended a total of only 13 flocks during the study period. In order to investigate the effects of the presence of gulls on levels of diving and surfacing synchrony, I regressed the index of synchrony (A^2) in relation to flock size separately for the two species in a log-log plot. Deviations from the regression line (or residuals) indicated whether individuals in a given flock tended to dive or surface at the level of synchrony expected for a flock of this particular size. Under the null hypothesis that the presence of gulls has no effects on synchrony, the sum of the deviations for the particular set of flocks attended by one or more gulls should be 0. If synchrony increased with the presence of gulls, the sum of the deviations would be a positive value.

Measuring dive and pause duration.—Using a stop watch, I measured dive and pause duration for all

video sequences to the nearest second. Dive duration refers to the amount of time spent underwater in one particular dive. Because individual identification was impossible, I started timing the length of a given dive when about half the birds had submerged and stopped when about half the birds had surfaced. This ensures that a median figure for dive duration is obtained for a given flock. Pause duration refers to the amount of time spent on the surface between foraging episodes. I started timing pause length when about half the birds had emerged from the preceding dive and stopped timing when about half the birds had submerged for the following dive. This process was repeated for all dives and surfacings in a given sequence. Timing dive events is not problematic once the arrhythmic flocks are excluded from the analysis.

Some of the dive sequences recorded in this study contained pauses in which scoters and goldeneyes entered a nondiving mode that involved mostly preening or social activities. Pause duration in these sequences became extremely long. I arbitrarily decided to include in the following analysis only those pauses that lasted less than 100 s in scoters and less than 55 s in goldeneyes. The reason for the different cut-off points in the two species is that dive duration in goldeneyes is shorter than that in scoters and, presumably, a shorter amount of time is needed for recovery. This excludes about five or six pauses in both species, but it is a conservative cut-off point, as the longest dives recorded are expected to have a recovery period of about 50 s in scoters and 20 s in goldeneyes (see below).

In order to investigate the extent to which scoters and goldeneyes completed physiological recovery after each dive, I used the technique developed by Ydenberg and Forbes (1988). One can use the regression of pause duration on dive length for each species to calculate deviation from the estimated pause duration in each dive cycle. The underlying assumption is that, on average, over the large number of dive cycles recorded in this study, scoters and goldeneyes were in physiological equilibrium. The regression equation, thus, can be used to estimate the average time necessary for full recovery from a dive of a given duration. Deviations from the regression line (DEVST, for short) are thus thought to be related to deviation from equilibrium. A positive value of this index indicates that individuals in the flock spend more time on the surface than is estimated to be required for full recovery. Similarly, a negative value of the index suggests that a shorter amount of time is spent at the surface than is needed for full recovery.

Statistical analyses.—Many of the variables that I measured (e.g. flock size) showed highly skewed distributions. For statistical purposes, I used a logarithmic transformation to normalize these distributions.

RESULTS

Diving and surfacing synchrony.—Overall, I analyzed diving behavior of 80 scoter flocks and

TABLE 1. Number of Surf Scoter and Barrow's Goldeneye flocks that showed random synchrony in diving and surfacing as a function of flock size.

Flock size	Diving		Surfacing	
	Fre- quency	<i>n</i>	Fre- quency	<i>n</i>
Surf Scoters				
3-10	15	42	24	42
11-20	1	23	0	23
21+	0	15	0	13
Total	16	80	24	78
Barrow's Goldeneyes				
3-10	6	26	5	24
11-20	0	21	1	18
21+	0	11	0	9
Total	6	58	6	51

58 goldeneye flocks, ranging in size from 3 to 60. Individuals in flocks of wintering scoters and goldeneyes tended to dive and surface in a highly synchronous fashion. Empirical distributions of interdive (or intersurfacing) intervals included many short intervals and fewer long intervals and this produced clumped distributions that deviated significantly from randomness. Nearly 80% of all scoter flocks and 90% of all goldeneye flocks showed strong diving synchrony (Table 1). At the same study site, Schenkeveld and Ydenberg (1985) reported a similar level of synchrony (around 85%) by scoter flocks.

The levels of diving and surfacing synchrony in a particular foraging flock were highly correlated. Figure 1 shows a log-log plot of the relationship between diving and surfacing synchrony in flocks of the two species. In these figures, the Anderson-Darling statistic obtained for each empirical distribution of interdive (or intersurfacing) intervals was used as an index of synchrony. Flocks that tended to dive in a highly synchronous fashion also tended to surface in a similar way. The slope of the regression line in the two species was not different from one and the intercept was close to zero. This suggests that most individuals in a given flock spent a similar amount of time foraging on the bottom.

Effects of flock size on diving synchrony.—The levels of diving and surfacing synchrony observed in foraging flocks of the two species were highly dependent on the number of birds present in the diving party. Table 1 shows that individual scoters and goldeneyes foraging in

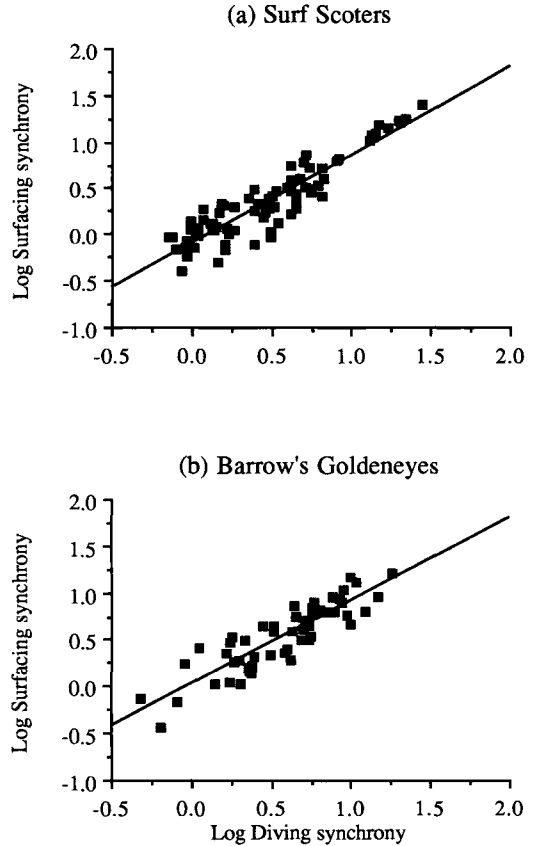


Fig. 1. Log-log plot of relationship between diving and surfacing synchrony in (a) scoter and (b) goldeneye flocks. Least-squares equation for scoter flocks: $Y = -0.092 + 0.95X$ ($n = 78$, $r^2 = 0.84$, $P < 0.0001$). Slope is not different from 1 ($SE = 0.047$, $t = 1.06$, ns). Least-squares equation for goldeneye flocks: $Y = 0.024 + 0.89X$ ($n = 53$, $r^2 = 0.77$, $P < 0.0001$). Slope is not different from 1 ($SE = 0.068$, $t = 1.62$, ns).

small flocks (<10 individuals) were less likely to dive and surface in synchrony than individuals in large flocks. In other words, the distribution of interdive (or intersurfacing) intervals in many of these flocks showed no deviation from the negative exponential distribution that was expected if birds behaved independently of one another. One reason for this is that the mean amount of time elapsed between successive departures by individual birds increased in these small flocks. Figure 2 shows that individual scoters and goldeneyes foraging in small flocks appeared to wait longer to follow a diving companion than individuals in large flocks. In general, diving synchrony in the two species increased with the number of birds

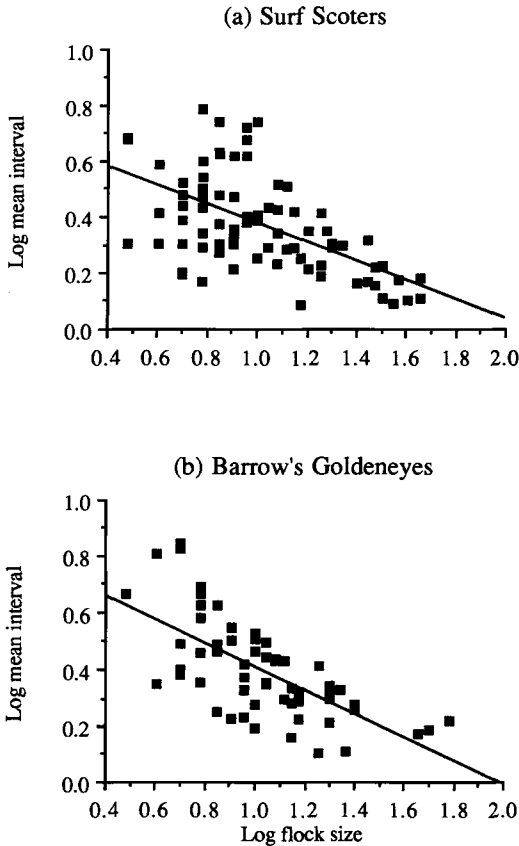


Fig. 2. Log-log plot of relationship between flock size and mean duration of intervals between successive departures in (a) scoter and (b) goldeneye flocks. Least-squares equation for scoter flocks: $Y = 0.72 - 0.34X$ ($n = 80, r^2 = 0.33, P < 0.0001$). For goldeneye flocks: $Y = 0.82 - 0.41X$ ($n = 59, r^2 = 0.45, P < 0.0001$).

present in the foraging flock. This probably reflects the fact that interbird distances tended to be shorter in the larger flocks (pers. observ.).

Effects of presence of gulls on synchrony.—In order to investigate the possibility that scoters and goldeneyes adjust diving behavior in the presence of kleptoparasitic gulls, I regressed the index of synchrony (A^2) in relation to flock size separately for the two species in a log-log plot. Residuals from the regression line indicated whether individuals in a given flock tended to dive or surface at the level of synchrony expected for a flock of this particular size. Table 2 shows deviations of the diving and surfacing synchrony index for the 13 flocks (7 scoter flocks and 6 goldeneye flocks) that were attended by one or more gulls. The levels of diving and surfacing synchrony in flocks of scoters and gol-

TABLE 2. Deviation of diving and surfacing synchrony index for a number of Surf Scoter and Barrow's Goldeneye flocks that were attended by one or more gulls. Mean deviation of synchrony index is not different from 0 ($P > 0.5$).

Flock size	Diving	Surfacing
Surf Scoters		
5	-0.15	0.06
6	-0.34	-0.25
6	0.44	0.52
7	-0.08	-0.16
7	0.14	0.00
10	-0.36	-0.25
18	-0.04	0.03
$\bar{x} \pm SE$	-0.055 ± 1.70	-0.007 ± 0.10
Barrow's Goldeneyes		
5	-0.43	-0.67
5	0.14	-0.10
9	0.26	0.31
9	0.25	0.05
20	-0.06	0.10
60	-0.12	-0.29
$\bar{x} \pm SE$	0.006 ± 0.11	-0.10 ± 0.14

deneyes were not affected by the presence of gulls in that changes in diving or surfacing synchrony showed no apparent directionality.

Dive and pause duration.—Figure 3 shows the distribution of dive duration in flocks of scoters and goldeneyes. Scoters spent more time underwater than goldeneyes, but it is not clear whether the larger scoters dove deeper or simply spent more time on the bottom searching for mussels than the smaller goldeneyes. In penguins, diving ability appears to be greater in larger animals (Butler and Jones 1982), and my findings may reflect the fact that large species have longer aerobic dive limits.

Overall, there was a weak tendency for pause duration to increase in relation to dive time spent underwater in the two species (Fig. 4). Because goldeneyes spent less time underwater than scoters, pause duration was shorter. In this analysis, I averaged dive and pause duration for each sequence of successive dive cycles by a flock. Hence, the sample size is the number of flocks observed and not the number of dive cycles recorded. This is advisable, as events happening during each dive cycle of a sequence probably are not independent of one another (e.g. birds usually dive at the same depth during a particular sequence).

Using the above relationships between dive and pause duration in the two species, I com-

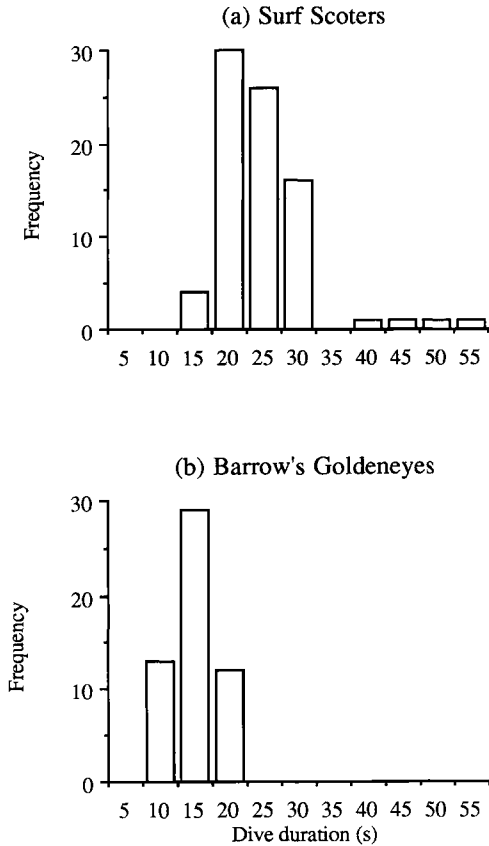


Fig. 3. Frequency distribution of dive duration(s) in flocks of (a) scoters and (b) goldeneyes. In scoter flocks, mean dive duration was $26.8 \pm \text{SD of } 6.7\text{s}$ ($n = 80$). In goldeneye flocks, mean dive duration was $17.3 \pm 2.8\text{ s}$ ($n = 54$). Numbers along X-axis represent the lower boundary of each interval.

puted the deviation (DEVEST) from the estimated pause duration for each dive cycle. In scoter flocks, DEVEST in the second dive of a sequence is significantly and positively related to that in the first dive cycle (Fig. 5). In scoters, flocks that spent less time on the surface in one dive cycle than is estimated to be needed for full recovery were also likely to show a negative deviation in the following dive cycle and vice versa. The relationship is weaker in flocks of goldeneyes. In this species, the deviation from estimated recovery time in one dive cycle appeared to be a poor predictor of current deviation in pause duration.

It is possible to examine the relationship between DEVEST in the current dive cycle with that in more than one previous dive cycle in

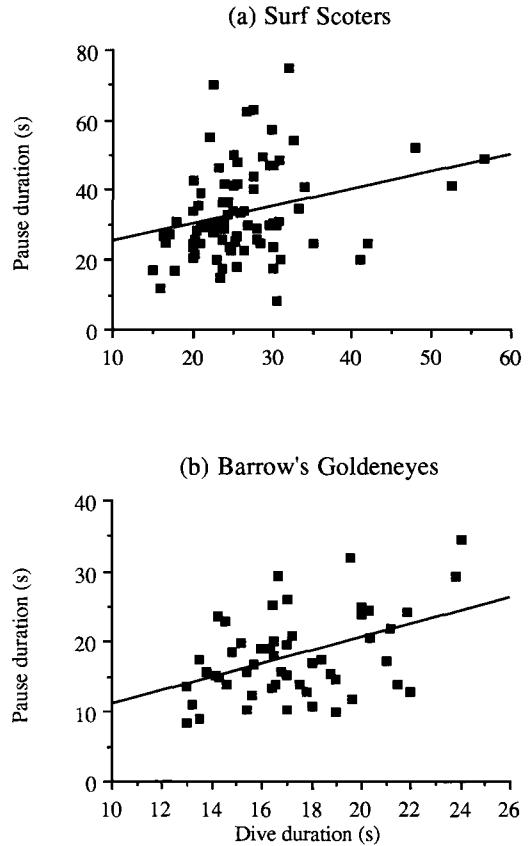


Fig. 4. Pause duration(s) plotted against duration(s) of the dive in (a) scoter and (b) goldeneye flocks. Least-squares equation for scoter flocks: $Y = 20.1 + 0.54X$ ($n = 71$, $r^2 = 0.08$, $P = 0.02$). For goldeneye flocks: $Y = 1.46 + 0.95X$ ($n = 52$, $r^2 = 0.20$, $P = 0.001$).

the particular set of sequences that included many successive dive cycles. I was able to monitor 22 flocks of scoters and 24 flocks of goldeneyes for at least four successive dive cycles. For the scoter data, DEVEST in the fourth dive cycle was correlated with that in the previous dive cycle but not with that in the previous two (Table 3). Together, the DEVEST in the three preceding dive cycles explained 35% of the variance in current DEVEST ($P < 0.05$). In goldeneyes, not surprisingly, DEVEST in the fourth dive cycle was not correlated with that of any previous dive cycle. Together, the DEVEST in the three preceding dive cycles explained only 7% of the variation in current DEVEST ($P > 0.6$). Why goldeneyes behaved in a different way is not clear and more research is needed.

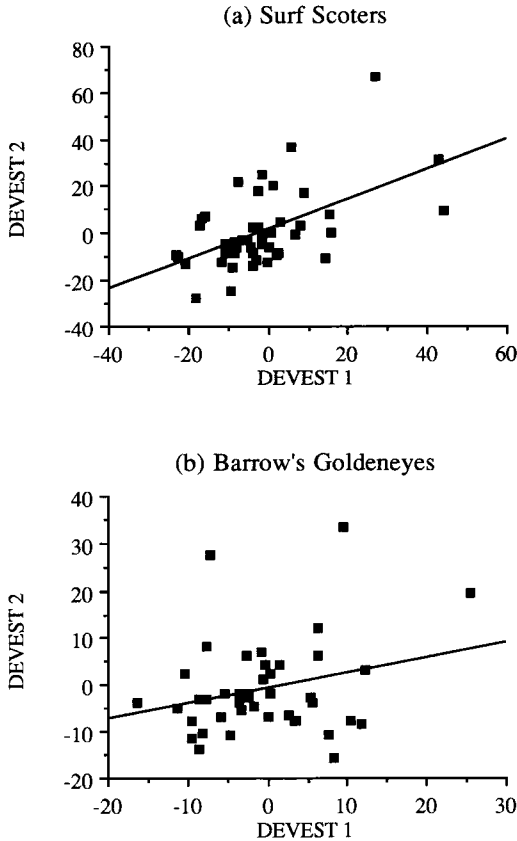


Fig. 5. Deviation from expected pause duration in second dive cycle of a sequence (DEVEST, based on dive-pause least-squares equations) in relation to DEVEST in the preceding dive cycle in (a) scoter and (b) goldeneye flocks. Negative values of DEVEST indicate shortage of surface time, and positive values indicate a surplus of surface time. Least-squares equation for scoter flocks: $Y = 1.83 + 0.63X$ ($n = 48$, $r^2 = 0.29$, $P < 0.0001$). For goldeneyes flocks: $Y = -0.71 + 0.33X$ ($n = 43$, $r^2 = 0.068$, $P = 0.09$).

Relationship between dive duration and synchrony.—It is conceivable that diving synchrony may be more difficult to maintain during longer dives. For instance, communication between birds may break down as divers forage longer. I regressed the index of surfacing synchrony as a function of average dive duration for each sequence recorded. Surfacing synchrony was independent of the amount of time spent underwater (scoter flocks, $F_{1,73} = 1.03$, ns; goldeneye flocks, $F_{1,48} = 0.68$, ns). In the range of dive durations observed, diving synchrony appeared to be maintained at the same level.

TABLE 3. Multiple regression of DEVEST in a dive cycle with that in three preceding dive cycles in Surf Scoters and Barrow's Goldeneyes.

Preceding dive cycle	Surf Scoters		Barrow's Goldeneyes	
	β coefficient	P	β coefficient	P
1	0.73	0.076	0.063	0.80
2	0.001	0.99	0.44	0.27
3	0.40	0.16	-0.13	0.72
n	22		24	
r^2	0.35		0.068	

DISCUSSION

Diving and surfacing synchrony.—The results of my study show that in Surf Scoter and Barrow's Goldeneye foraging flocks, individuals tend to dive and surface in a highly synchronous fashion. The levels of diving and surfacing synchrony found in scoter flocks are similar to those described by Schenkeveld and Ydenberg (1985).

In contrast to findings by Schenkeveld and Ydenberg (1985), scoters and goldeneyes in my study showed no tendency to alter diving behavior in the presence of kleptoparasitic gulls. As opposed to the aforementioned report, kleptoparasitism happened infrequently, perhaps because alternative sources of food were readily available to gulls. It may be that scoters and goldeneyes alter diving behavior in the presence of gulls only when the risk of being robbed is high. The fact that diving synchrony remains at a high level despite presumed variations in kleptoparasitism risk suggests that it is likely that more than one kind of benefit underlies synchronous diving.

In the two species, one important source of variation in the level of synchrony exhibited by different flocks is diving-party size. Diving synchrony increases with flock size. Submersion schedules, thus, are more temporally clustered in large groups. One possible interpretation of the increase in synchrony with flock size is that individual movement is restrained to a greater extent in large flocks. In large groups, where interbird spacings are usually short, individuals cannot move independently of one another while traveling to and from the bottom, and synchrony may help to maintain cohesion during the foraging episode. In order to illustrate this point, consider the consequences of asynchronous diving in large flocks. In a large

group, an increase in the duration of intervals between successive departures may mean that by the time the last few individuals have submerged, a number of birds would be on the verge of returning to the surface. Submerging and surfacing individuals, thus, would have to swerve to avoid one another, with the potential risk of crashing or losing the prey in the process. Avoiding obstacles has been shown to influence decisions taken by foraging European Starlings (*Sturnus vulgaris*; Cuthill and Guilford 1990), and a similar phenomenon may be at work in diving flocks.

I suggest that synchrony may be the expression of a cooperative pattern of group exploitation. This may be particularly important when individuals dive for mussels. Mussels are very abundant, but apparently not all mussels are available to foragers. Mussels on the edge of openings in the mussel bed are especially prone to capture (Schenkeveld and Ydenberg 1985), and this probably reduces the area over which a foraging flock operates. Maneuverability is presumably inversely proportional to flock size, and this may explain why a random distribution of intervals between successive departures has only been observed in small groups. One way to test the interference hypothesis would be to allow groups of different sizes to forage over food patches of different sizes. The expectation is that diving synchrony within a given flock size category would vary as a function of patch size.

Under different circumstances, synchrony may actually be disadvantageous. For instance, intraspecific kleptoparasitism would likely decrease the tendency to follow diving companions quickly. Diving synchrony may also be detrimental to birds foraging on rare and unevenly distributed prey. As mentioned earlier, synchrony tends to reduce variance in bottom time. However, search time for scattered prey is likely to be variable in a group. Hence, synchrony may curtail dive duration for unsuccessful foragers, thereby reducing prey intake. Generally, synchrony is likely to be dependent on a host of factors, including patch type and size.

Dive and pause duration.—In scoters and goldeneyes, the dive-pause relation is steeper than that found in the piscivorous Western Grebe (Ydenberg and Forbes 1988), but similar to that found in Common Eiders, a species that forages mainly on sessile prey (Ydenberg and Guille-

mette 1991). Ydenberg (1988) suggested that differences in dive-pause relations may be related to diet. Short pauses by piscivores are thought to be beneficial because transient schools of fish can escape between dives. The fact that grebes alternate disproportionately long and short periods on the surface between successive dive cycles supports the idea. If this interpretation is correct, then one expects the tendency to adjust pause duration in this fashion would be reduced or absent in species foraging on sessile prey. As a consequence, divers such as scoters, eiders and goldeneyes should complete more of the physiological recovery after one particular dive than birds like grebes feeding on mobile prey.

The analysis of the deviation from expected pause duration in scoters and goldeneyes shows that the tendency for successive dive cycles to have a similar DEVEST is weak. Moreover, the effect can only be traced back to at most one dive cycle. The results suggest that in each dive of a sequence there is only a weak tendency for either scoters or goldeneyes to spend more or less time on the surface than is estimated to be needed for full recovery. This supports the idea that divers foraging on sessile prey should complete more of the physiological recovery after each dive than divers foraging on mobile prey.

Although the tendency to adjust pause duration in a series of dive cycles is weak in scoters and goldeneyes, it is not absent. Ydenberg and Guillemette (1991) observed a similar pattern in Common Eiders. One possible interpretation is that small adjustments in pause duration are useful to birds feeding on sessile prey when the sequence of dive cycles may be interrupted by external causes. In the case of scoter and goldeneye flocks foraging along the seawall in Stanley Park, the presence of passersby close to the shore often meant that a series of dive cycles would be postponed until after people moved away. Under these circumstances, it may be useful to shorten pause duration in a few successive dive cycles in order to reduce time spent along the seawall. Birds foraging under more natural conditions also would benefit from similar adjustments. Foraging in flocks of diving birds conceivably can be interrupted by a number of factors, such as the presence of a predator and changes in local foraging conditions (e.g. rapid formation of ice pack on a patch of clear water in the case of winter foraging in Common Ei-

ders). Admittedly, the scope of such adjustments is possibly much reduced compared to that found in divers foraging on mobile prey.

ACKNOWLEDGMENTS

I thank Ron Ydenberg and Peter Arcese for useful discussions, and Alex Fraser for much needed help with the video equipment. I was supported by an NSERC postdoctoral fellowship and by an NSERC operating grant to Ron Ydenberg.

LITERATURE CITED

- BUTLER, P. J., AND D. R. JONES. 1982. Comparative physiology of diving in vertebrates. Pages 179-364 in *Advances in physiology and biochemistry*, vol. 8 (O. E. Lowenstein, Ed.). Academic Press, New York.
- CUTHILL, I., AND T. GUILFORD. 1990. Perceived risk and obstacle avoidance in flying birds. *Anim. Behav.* 40:188-190.
- MCKINNEY, F. 1965. The spring behavior of wild Steller's Eiders. *Condor* 67:273-290.
- SAVARD, J.-P. L., AND J. N. M. SMITH. 1987. Inter-specific aggression by Barrow's Goldeneyes: A descriptive and functional analysis. *Behaviour* 102:168-184.
- SCHENKEVELD, L. E., AND R. C. YDENBERG. 1985. Synchronous diving by Surf Scoter flocks. *Can. J. Zool.* 63:2516-2519.
- STEPHENS, M. A. 1974. EDF statistics for goodness of fit and some comparisons. *J. Am. Stat. Assoc.* 69:730-737.
- STEWART, P. A. 1967. Diving schedules of a Common Loon and Oldsquaw. *Auk* 84:122-123.
- WILSON, R. P., M. P. T. WILSON, AND L. MCQUAID. 1986. Group size in foraging African Penguins (*Spheniscus demersus*). *Ethology* 72:338-341.
- YDENBERG, R. C. 1988. Foraging by diving birds. Pages 1832-1842 in *Acta XIX Congressus Internationalis Ornithologic* (H. Ouellet, Ed.). Ottawa, Ontario, Canada, 1986. National Museum of Natural Science, Ottawa.
- YDENBERG, R. C., AND L. S. FORBES. 1988. Diving and foraging in the Western Grebe. *Ornis Scand.* 19:129-133.
- YDENBERG, R. C., AND M. GUILLEMETTE. 1991. Diving and foraging in the Common Eider. *Ornis Scand.* 22:349-352.