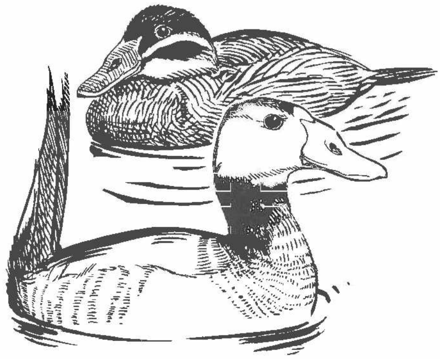
Rafting as an antipredator response of wintering White-headed Duck *Oxyura leucocephala*



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The flocking behaviour of White-headed Ducks was studied at their most important wintering site at Burdur Gölü in western Turkey. Ducks fed singly by night and day in a prey-rich environment, but gathered during daylight into rafts to preen, rest and sleep, when inter-bird distances were significantly less than when feeding. Hence, rafting behaviour appears to have a predation avoidance function in the White-headed Duck, and is not related to foraging efficiency. Nearest neighbour distances declined rapidly in response to attacks from their most common predators, Herring Gulls, hence predator detection was an unlikely cause of rafting. White-headed Duck resorted to alert postures and eventually dived to avoid attacking gulls, so it was considered that predator deterrence was not responsible for flocking behaviour. Gulls singled out individual ducks which they pursued until exhausted, and were less successful where individuals could not be isolated. The length of time gulls spent harrying flocks of White-headed Duck was positively correlated to group size, and the proportion of ducks escaping from a detected predator was greater in large groups than smaller ones, hence we suggest that rafting in the White-headed Duck is primarily to dilute the predation risk from its major predator, large gulls. However, individuals also benefit from the predation confusion effect of escape by diving in association with groups of others.

Keywords: Ecology, Disturbance, Behaviour, Threatened Species, White-headed Duck, Herring Gull

White-headed Ducks *Oxyura leucocephala* are specialist feeders, diving for abundant chironomid larvae in the sediments of saline or endorreic lakes (Torres & Arenas 1985, Green & Anstey 1992). Prey location is largely tactile, and foraging takes place mainly at night, although daytime feeding does occur (Amat 1984, Green *et al.* 1993). Although wintering White-headed Ducks are frequently encountered singly, they also aggregate into large rafts (Green *et al.* 1993).

Rafting behaviour may result either from an opportunity to reduce predation risk or enhance individual condition (since a group of individuals may reflect a good feeding area which is worth joining, e.g. Krebs 1974, Pöysä 1987 or may share vigilance which increases individual foraging duration, e.g. Hamilton 1971, Fox & Madsen 1981). Reduction of predation risk to an individual may occur through a number of mechanisms, such as increased predator detection as a result of group vigilance (Pulliam 1973, Caraco 1979, Bertram 1980), predator deterrence (e.g. mobbing, Hoogland & Sherman 1976), predator confusion (e.g. Neill & Cullen 1974, Curio 1976), and avoidance of becoming a victim as a result of dilution of the predators effects (Foster & Treherne 1981, Ryan *et al.* 1982, Turchin & Kareiva 1989).

Generally, encounters between predators and prey animals are relatively rare and hence difficult to study. However, during a study of the White-headed Duck at its most important wintering site in Turkey, adult and sub-adult Herring-type Gulls *Larus argentatus* in this paper we use the term 'Herring Gull' to embrace both *L. cachinnans* and *L. armenius* were regularly witnessed attacking White-headed Ducks and occasionally Coot *Fulica atra* during daylight hours and at least one successful kill was witnessed (Green *et al.* 1993).

In this paper, we assess the adaptive advantages of rafting behaviour to the White-headed Duck in the context of theories relating to such behaviour. In particular, we assess whether aggregations are a response to foraging opportunity or predation pressure.

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Methods

Study area

Burdur Gölü is a closed basin saline lake of 130-200 km^2 at 845 m above sea level in south-west Anatolia, Turkey (37°43'N 30°15'E). It has been the wintering site for more than 70% of the world population of White-headed Ducks (Anstey 1989, Green & Anstey 1992) and as such has been designated an Important Bird Area (Grimmett & Jones 1989) and a Ramsar wetland of international importance. The site faces numerous wildlife conservation problems, including the effects of accelerating sedimentation, drought and pollution and this study forms part of a wider programme of research carried out at the site by The Wildfowl & Wetlands Trust (see Green *et al.* 1993). At the time of this study, the White-headed Ducks fed on the superabundance of Chironomid larvae (up to 47,000 m^{-2}) in the shallow waters of the lake (generally less than 17 m depth) and were therefore mainly confined to areas within 200 m of the shoreline.

Behavioural observations

Behavioural observations were carried out on White-headed Ducks between 10 February and 4 March 1993 at four study sites on the lake. Diurnal and nocturnal time budget data were collected in three hour sessions during 0030-0329 hr, 0330-0629 hr, etc. Observation sessions were alternated between sites in such a way that the full 24-hour cycle was covered at each site over a period of four days. This cycle was completed twice for each site, with a total of 192 hours of observations. The presence and activity of large gulls were also recorded, as were the specific responses of White-headed Ducks to their predators.

During diurnal observations, the number and sex of birds in the study area were noted at the beginning of the session and then flock scans were conducted every 15 minutes using a x20 wide angle Kowa telescope. Using a dictaphone, the sex, behaviour and the distance to the nearest neighbour was recorded for each bird encountered during a scan. Nearest neighbour distances were estimated in metres; to reduce observer bias, inter-bird distance data are only presented from one observer (ADF). When the nearest neighbour was a different species, the distance to the nearest White-headed Duck was also noted.

Nocturnal behaviour was observed using a Davin Optical Ltd. Modulux 130 image intensifier fitted with a Tamron 300 mm f2.8 lens and external infra-red light source. Fewer birds were located at night, so continuous focal observations were recorded (using an event recorder computer package or stopwatch) for 30 minutes, or less if the bird swam out of sight. Different birds were selected for observation, choosing males and females/immatures (the latter are not easily distinguishable in the field) alternately when possible. The sex and distance from the shore were recorded for each bird observed.

Behavioural categories recorded were: *Feeding* (diving and inter-dive interval); *Sleeping* (resting behaviour with head-on-back and eyes open or closed. Birds moving while in the sleeping posture were included); *Loafing* (resting behaviour with eyes open without head-on-back); *Preening*; *Swimming*; *Alert* (head-up, extreme head-up and head-up-tail-up); *Flying*; *Social Interaction* (intra-and interspecific interactions). Sleeping and loafing were combined as *Resting*, while swimming and flying were combined as *Movement*.

Results

White-headed Duck aggregation in relation to individual behaviour

There were no significant differences between the frequency distributions of inter-bird distances of male and female/immature White-headed Ducks indulging in the four major activities (preen $\chi^2_6 = 7.67$, $P > 0.05$; sleep+loaf $\chi^2_6 = 5.83$, $P > 0.05$; feed $\chi^2_6 = 3.73$, $P > 0.05$; swim $\chi^2_6 = 3.48$, $P > 0.05$), so data from both groups were combined for the following analysis.

During daylight hours, White-headed Ducks dispersed whilst feeding, when more than 60% of feeding birds were more than 5 m from their nearest neighbour. Ducks showed intermediate distributions whilst swimming, but were highly aggregated during periods of active preening and when sleeping (when more than 80% of over 11,500 bird observations involved preening/sleeping individuals within 1 m of another White-headed Duck, **Figure 1**). Whilst actively feeding at night, White-headed

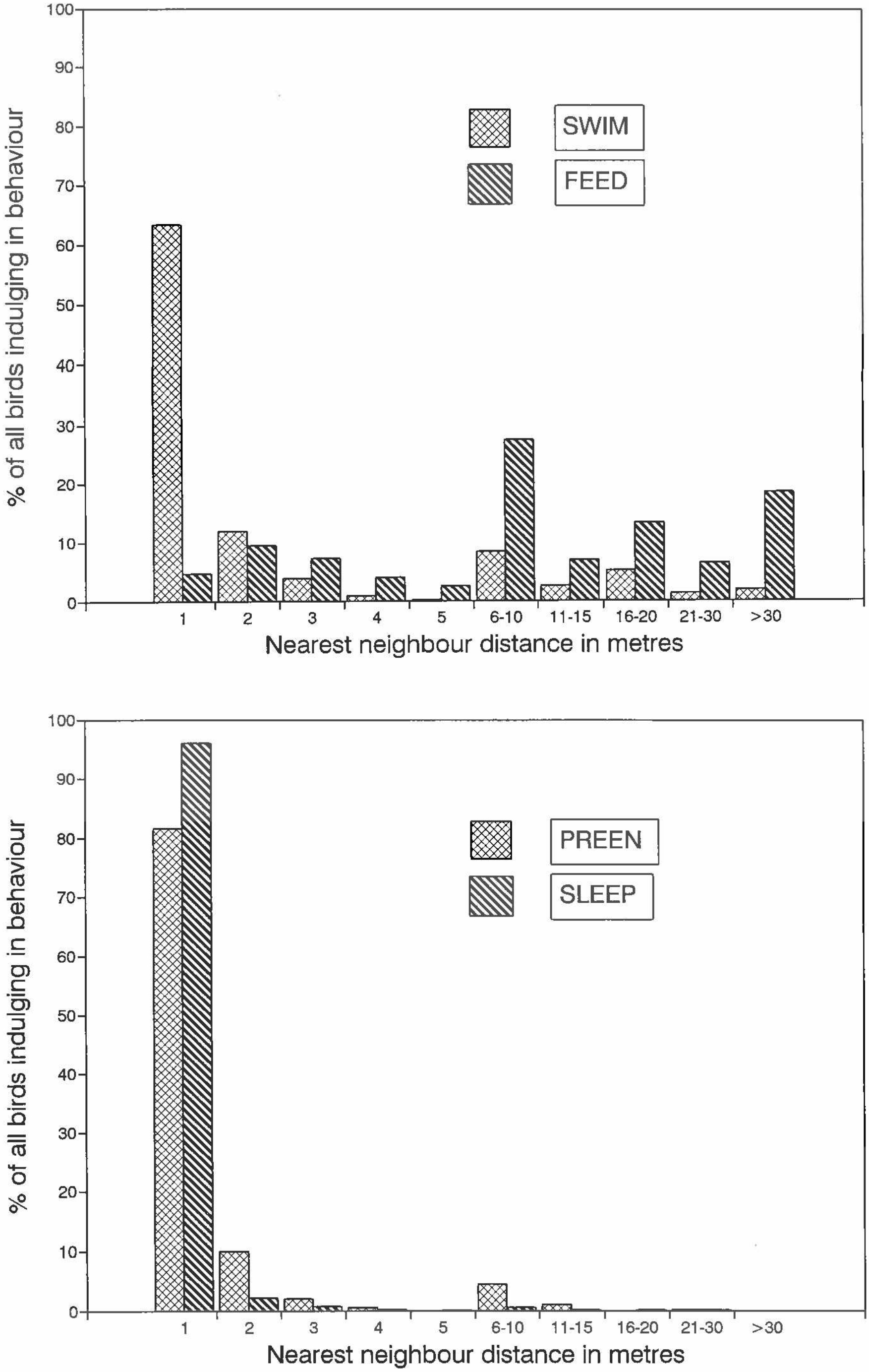


Figure 1. Frequency distributions of White-headed Duck nearest neighbour distances in relation to behaviour. Only data from one observer (ADF) are presented to minimise observer error. Upper graph shows frequency distributions of nearest neighbour distances during feeding (n = 893) and swimming (n = 310), the lower graph during preening (n = 201) and sleeping (n = 11,322). The frequency distributions of all four behavioural categories differ at $P < 0.001$, except for preen and swim which were not significantly different ($\chi^2_{10} = 18.06$, $P > 0.05$). Data from Burdur Gölü, Turkey, February/March 1993.

ducks were always watched foraging alone, indeed it was rare to encounter more than one individual in the field of view of the nightscope. No rafts of White-headed Ducks were encountered at night, when sleeping comprised only 2.8% of all nocturnal observation time, although two birds were seen sleeping amongst a flock of Coot on one occasion. Hence throughout the entire 24 hour period, White-headed Ducks foraged alone or in small dispersed groups, but roosted and preened in rafts.

Gull attacks on White-headed Ducks

Larus argentatus gulls were recorded attacking White-headed Duck during 25% of the 24 3-hour daylight observation periods at three of the four study sites. Although attacks were occasionally observed on flocks of Coot, these were unsuccessful because of the very tight flocking behaviour of this species and casual observation suggested a preference for attacking the smaller White-headed Ducks rather than other species. No attacks were witnessed on adjacent roosting rafts of Pochards *Aythya ferina*, for example. Since *Larus argentatus* gulls were only active by day, no attacks on White-headed Duck were recorded during darkness.

Attacks were initiated by single adult and sub-adult gulls, or groups of up to four individuals opportunistically as they flew past sites occupied by White-headed Duck. Gulls dived amongst ducks, attempting to split them into smaller groups. Most of these groups swam quickly away, dived synchronously or took to the wing and flew elsewhere. Ducks in the focus of the attack typically dived, and were frequently separated from the main group when they subsequently surfaced. This was in contrast to Coot where no birds were seen to be split from the tight flock formed in response to the presence of gulls. Gulls then targeted these single White-headed Ducks which would react by swimming away from the gulls, and it was this isolation which apparently enables the gull to make the repeated attacks on one individual which eventually kills the duck. The only successful attack witnessed began on 10 February at 1340 h and led to the isolation of a female/immature duck. As it swam for the shore, it was followed by the gull which repeatedly took off and dived at the duck as it surfaced. The duck would dive to avoid such attacks, but eventually tiring, it was grabbed and shaken when it surfaced alongside the gull. This cycle was repeated several times, with the female/immature making a final escape dive at 1430 h but it was finally killed after a further blow to the head at 1443 h. The gull subsequently ate the duck.

White-headed Duck responses to predator presence

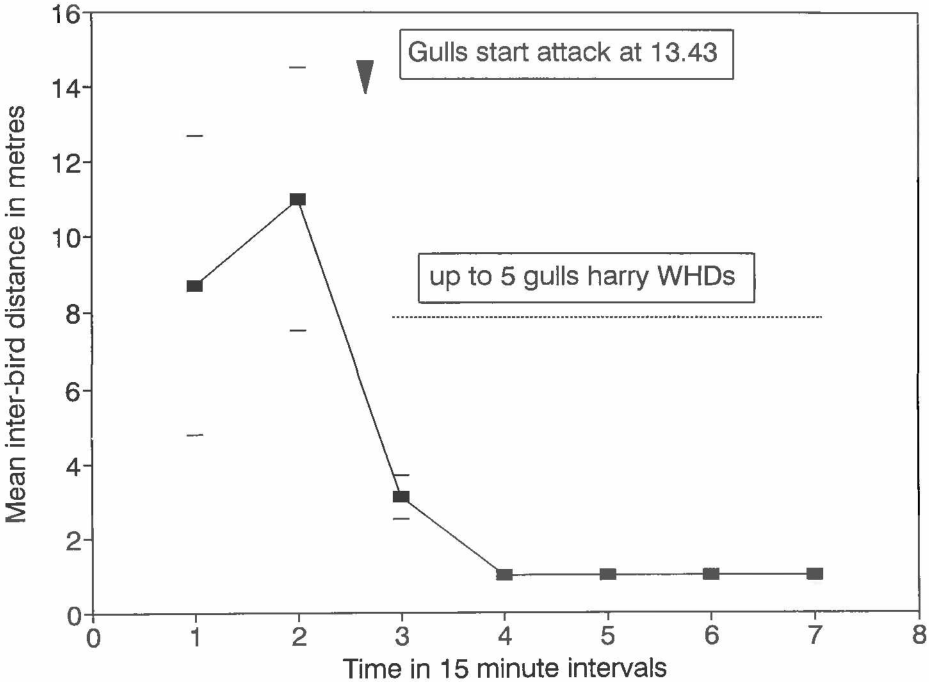
Gulls stimulated a strong behavioural response from White-headed Duck, which reacted as if they identified them as major predators. For example, at 1353 h on 2 March, 324 ducks were present with 80% resting when 3-5 gulls began repeated attacks. All ducks immediately assumed the head-up-tail-up alert posture (Cramp & Simmons 1977), and over 80% had flown off from the study site by the time gulls left at 1528 h.

Typically, however, White-headed Duck showed rapid aggregation in response to attacks from gulls (e.g. **Figure 2**). Gull attacks were found to result in significant increases in alert and locomotory behaviours and significant decreases in feeding behaviour (**Table 1**).

Predator dilution - is it worth being in a larger flock?

There was a significant and positive correlation between the time in minutes spent by gulls harassing White-headed Duck flocks and flock size (TIME=0.114FLOCKSIZE + 10.51; r_{12}=0.92, P<0.001). However, the probability of escape of birds from the immediate vicinity of attacking gulls was greater amongst large flocks than small ones, because the proportion of a flock which flew away from the immediate vicinity of attacking gulls was significantly correlated with flock size (%FLY=0.320FLOCKSIZE -10.09; r_{11}=0.87, P<0.001).

Gull activity followed a similar pattern on most days - the birds dispersed from roosts in the early morning and appeared to exhibit bimodal activity patterns (**Figure 3**), with peaks in appearance at White-headed Duck feeding areas in the morning (0900-1000) and early afternoon (1300-1500). This is also reflected in the timing of attacks on White-headed Duck (**Figure 3**), which tended to aggregate into large flocks from first light in the morning and spent most time resting during the pe-



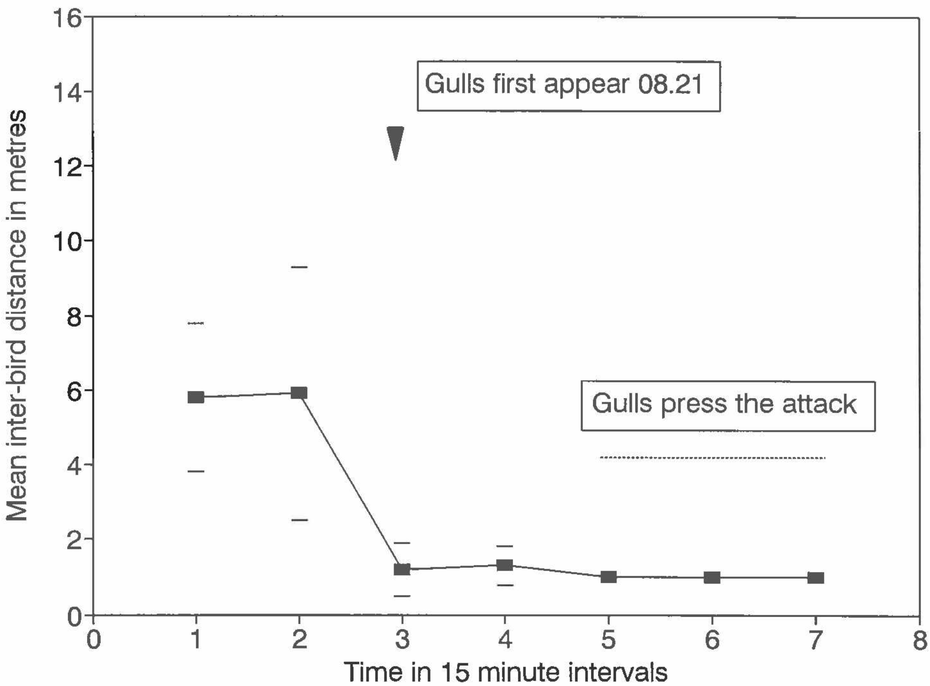


Figure 2. Three examples of the responses of White-headed Duck (WHD) to attacks by gulls, showing change in mean inter-bird distance before and after the attacks on three different dates (top: 26 February; bottom: 27 February; next page: 2 March 1993). Values indicate means± 95% confidence intervals. Arrows indicate commencement of attacks by gulls, dotted lines indicate duration of harassment. Data from Burdur Gölü, Turkey, February/March 1993.

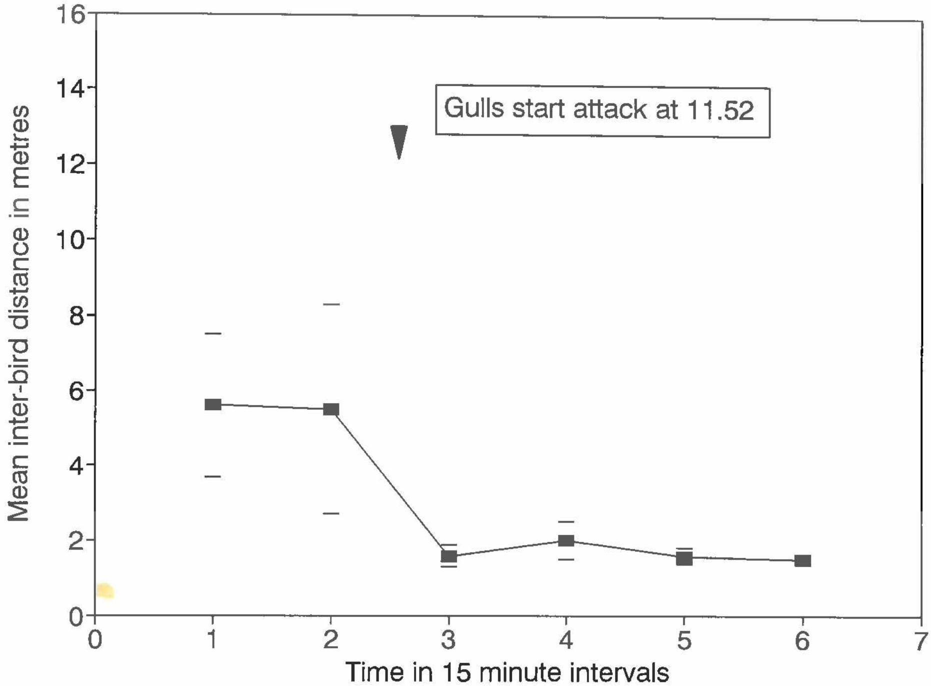


Figure 2 ***continued from previous page.***

riod 0900-1500 (Green *et al.* 1993). However, there was no significant negative correlation between the time White-headed Ducks spent resting and the frequency of gulls present in the same area based on hourly mean values (r_{13}=0.52, P <0.05), as might have been expected from the relationship shown in **Table 1**. There was no correlation between White-headed Duck flock size and the frequency of gulls present based on hourly mean values from two of the sites for which detailed observations were available (r_{13}=0.32, P > 0.05; r_{13}=0.23, P > 0.05).

Discussion

These observations show that White-headed Duck foraging at Burdur Gölü disperse away from resting flocks to feed as individuals. While we cannot be certain that large rafts do not form close to areas of high chironomid densities, the hypothesis that foraging efficiency is directly enhanced by the process of rafting can be rejected, since virtually no feeding took place in rafts. By contrast, *Larus argentatus* type gulls apparently exert a strong influence upon White-headed Duck behaviour, more so than the effects of human hunting which were a source of greater mortality (see dis-

Table 1. Activity budgets for White-headed Duck with and without the effects of *Larus argentatus* gull attacks, February/March 1993, Burdur Gölü, Turkey. Analyses are conducted on paired means for scans with and without gull attacks for the eight sessions where attacks were observed, using a one tailed Wilcoxon Matched-Pairs Signed-Ranks test. N_t = N for Wilcoxon Test, i.e. number of matched pairs in which there is a difference; T = Wilcoxon Statistic, S.D. = Standard Deviation, * indicates P < 0.05.

	With gulls		Without gulls				
Behaviour	Mean	S.D.	Mean	S.D.	N_t	T	P
Alert	21.8	8.9	0.1	0.18	5	0	0.030*
Movement	15.9	12.1	5.1	3.3	8	1	0.011*
Feeding	8.7	10.4	18.8	11.1	8	3	0.021*
Resting	57.0	20.9	73.7	10.7	8	8	0.092

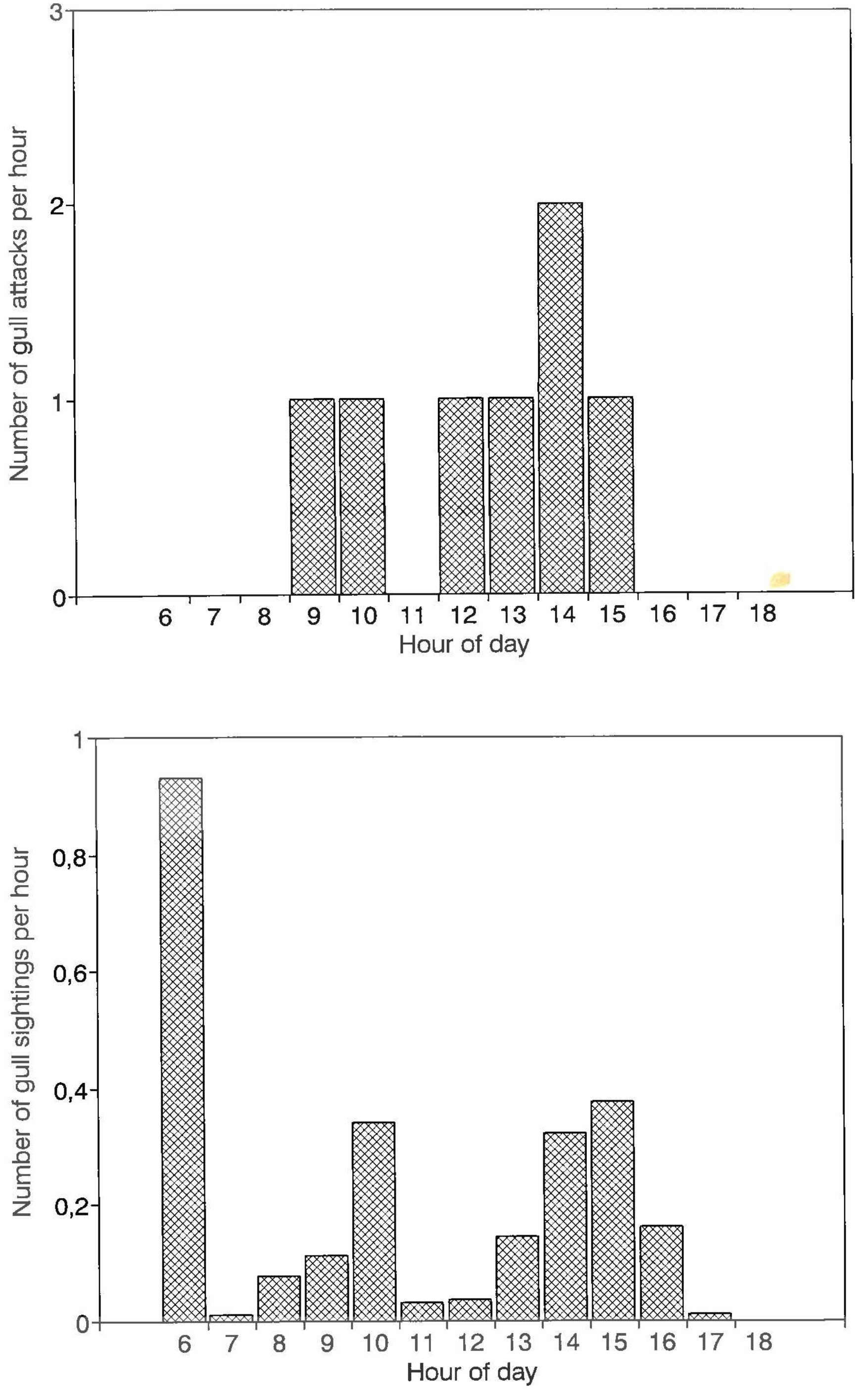


Figure 3. Upper: Diurnal activity of Herring Gulls *Larus argentatus* based on frequency of records of birds overflying White-headed Ducks per hour, February/March 1993, Burdur Gölü, Turkey. The abnormally high peak in the early morning reflects dispersal of gulls from night-time roosts, although there was no such dramatic evening return roost flight during the hours of daylight. Lower: Diurnal distribution of attacks by gulls on rafts of White-headed Ducks, during the same period.

cussion in Green *et al.* 1993). Duck dispersal to feed on their own increases individual isolation, increasing the risk of predation by gulls. Adult and immature large gulls regularly attacked White-headed Ducks during daylight hours. Gulls (singly or in groups of up to five individuals) harassed individual ducks, causing them to dive until exhausted, whereupon successful predation could be achieved. Such hunting behaviour has been observed amongst White-tailed Eagles *Haliaeetus albicilla* (Cramp & Simmons 1980, Love 1983), whose presence may explain the rafting behaviour of Pochard at Burdur Gölü (Pochard were not witnessed being attacked by gulls). The physical features of particular parts of the lake may influence the ability of gulls to corner White-headed Ducks successfully. Shallow bays may represent the areas with the highest probability of successful predation, but our sample sizes were too small to assess this factor. Greater Black-backed Gull *Larus marinus* predation of injured Ruddy Ducks *Oxyura jamaicensis* occurs in Britain, where this Stifftail also suffers gull attacks at evening roosts (BH pers obs.).

Attacking gulls caused scattered birds and smaller groups to coalesce into larger rafts, demonstrating that aggregation is actually a result of the presence of a predator; hence enhanced predator detection is not a primary cause of flocking behaviour. Attacking gulls usually dived into flocks, attempting to split them into groups, invariably causing the ducks to dive or swim away from the predator, with no sign of aggressive or mobbing behaviour focused upon their attacker. Hence, predator deterrence cannot be responsible for the gathering of White-headed Ducks.

The remaining two hypotheses which might explain rafting behaviour (predator confusion and the dilution effects of grouping) both predict that large groups ought to be safer to individual group members than smaller ones. If this were the case, individuals should respond to increasing risk of predation by resorting to larger groups. However, in the present study, no such trend could be found. It may be that flock size response may operate at a site level, with White-headed Ducks experiencing characteristic levels of gull presence depending on the nature of the site. For instance, at one of the study sites, close to the effluent discharge from a milk factory, up to 300 gulls were attracted to a beach for roosting. Here, White-headed Ducks foraged in small groups, yet no attacks were witnessed here at the one site where gull presence was both frequent and most predictable. Unfortunately, sample sizes from individual sites were too low to investigate the hypothesis that such site characteristics affect both duck and gull behaviour.

Gull predation depends on isolation of individual birds which can then be attacked repeatedly, hence the survival value of being in a large group of ducks may result either from the reduction in the individual probability of being killed by 'hiding' amongst many more potential victims or from the effects of predator confusion which a larger group of individuals confers. The predictions arising from these two hypotheses could be tested by comparing the observed predation rates amongst flocks of different size. Under the predator dilution hypothesis, absolute predation rates on flocks potentially could be independent of flock size, whilst the predator confusion hypothesis predicts lower success rates amongst larger flocks. Unfortunately, too few successful predation events were fully witnessed to differentiate these two hypotheses. However, we can make further predictions based on indirect support for these alternative factors. For instance, if gulls learned from past encounters with ducks, and success rates were highest amongst small groups, it might be expected that gulls would invest longer periods in harassing smaller flocks. Our observations suggest the contrary, with gulls maintaining harassment of larger groups for longer before giving up. Since escape flights from attacks on larger rafts were actually more frequent than in smaller groups, this suggests that some predator dilution effects may thus accrue to individual group members. Equally, gulls may attack larger flocks because they offer a larger stimulus, and the persistence of ducks may protract the attacks for the same reason.

The gulls may have learned that persistence in attacking very large rafts of White-headed Ducks is more effective at putting large numbers of birds to flight and hence singling out weaker individuals which are less likely to fly or dive away. From direct observation, it was clear that gulls were confused by both large or small numbers of birds all diving synchronously away from their attacker, surfacing in different directions. The ability of the gulls to concentrate on the pursuit of one individual was therefore diminished in all group sizes.

We therefore conclude that the predation dilution and predator confusion functions of rafting behaviour may both play a role in the aggregation behaviour of White-headed Ducks wintering at Burdur Gölü. We suggest that in large groups, healthy White-headed Ducks are more likely to escape by flight from attackers than in smaller ones, and that diving away from marauding gulls is an effective means of confusing the predator, distracting the gulls from following individuals which might otherwise be pursued until exhausted. For the gulls, there may be a benefit in attacking large groups, since this strategy is more likely to put birds to flight, exposing the weaker birds which are more likely to seek the protection of larger aggregations. Hence, optimal flock size may be the result of a trade-off between (a) the decreasing probability of each bird being a target during an attack as a result of dilution with increasing flock size, (b) the increasing probability of an attack and its duration with increasing flock size and (c) the physical nature of the White-headed Duck feeding site.

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