

# Time–activity budgets and site selection of White-headed Ducks *Oxyura leucocephala* at Burdur Lake, Turkey in late winter

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*Diurnal and nocturnal time–activity budgets were compiled for White-headed Ducks at their most important wintering area, Burdur Lake in Turkey, during February and March 1993. During the day, ducks spent 28% of the time feeding, 57% resting, 11% in locomotion, 4% preening and 1% in alert behaviour. No courtship behaviour was observed. Resting peaked in the middle of the day. As wave-height increased, feeding and swimming increased and resting decreased. At night, 92% of time was spent feeding. Sites used by White-headed Ducks held a higher biomass of food items (benthic chironomid larvae) than other parts of the lake. Movement of individuals and marked differences in diurnal time budgets occurred between sites, as birds concentrated in flocks for resting and dispersed to feed. The proportion of birds resting increased with the number of birds present, both within and between sites. Feeding was concentrated at those sites supporting a higher biomass of chironomids for a given depth.*

The White-headed Duck *Oxyura leucocephala* is globally threatened<sup>1,2</sup> and is the only stiff-tail (Oxyurini) native to the Palearctic.<sup>3</sup> Most of the global population winters at Burdur Lake in Turkey.<sup>4,5</sup> Nothing was known about the ecology and behaviour of the ducks at this lake prior to the current study, yet Burdur Lake is suffering major environmental change as a result of human activities and drastic declines have occurred recently in the numbers of White-headed Ducks and other waterbirds.<sup>5,6</sup>

This study was designed to assess how White-headed Ducks use the lake and to identify possible causes of the decline in wintering numbers. We aimed to quantify White-headed

Duck behaviour at several sites on Burdur Lake, by both day and night. Many duck species are largely nocturnal outside the breeding season,<sup>7–9</sup> but the only previous study of time–activity budgets in White-headed Ducks was limited to daylight hours.<sup>10</sup> We aimed to compare duck behaviour at the two points of the lake most affected by inputs of organic pollution with that at other, less polluted sites.

We also aimed to establish the influence of variation in food supply on the behaviour and distribution of White-headed Ducks on the lake. Other wintering ducks (but not stiff-tails) have been shown to forage selectively at sites offering higher food densities.<sup>11–15</sup> Finally, we aimed to identify the influence of weather on White-headed Duck behaviour, which may obscure effects of food supply or other

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differences between study sites. Weather has a strong influence on the behaviour of wintering Anatidae.<sup>8,16</sup>

## STUDY AREA

Burdur Lake is a brackish, closed-basin lake without emergent vegetation and with an area of about 140 km<sup>2</sup>, in southwest Anatolia, Turkey (37°43'N 30°15'E, Fig. 1).<sup>5</sup> White-headed Ducks concentrate at the lake in winter and, although present throughout the year, do not breed there.<sup>5,6</sup> During this study, the diurnal temperature of surface waters ranged from 3.4 to 10.9°C.

Four sites where White-headed Ducks were present continuously were selected for intensive observations. These included two 'polluted' sites along the eastern shore, in bays where a milk factory (MF) and sugar factory (SF) discharged organic wastes into the lake. We wanted to assess the influence of these major pollution sources<sup>5</sup> on the birds. In addition, two sites holding concentrations of White-headed Ducks on the west shore were selected, a southwest bay (SW) and a holiday beach (HB) (Fig. 1). SW and HB were over 3 km

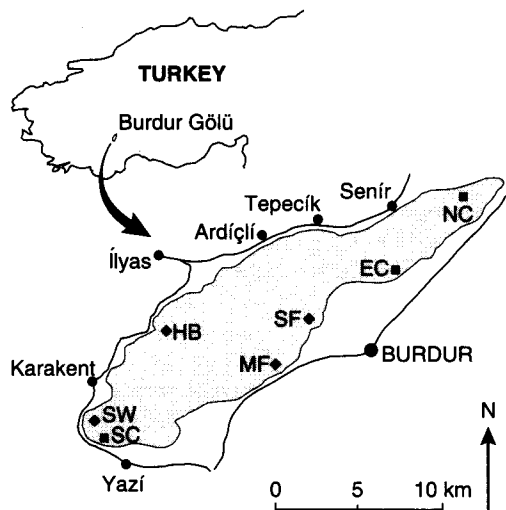
from known pollution sources<sup>5</sup> and were selected partly because of ease of access by road. Together, these four sites held about 25% of the White-headed Ducks on the lake.<sup>5</sup> The potential food supply was also studied at three control sites not used by White-headed Ducks. These were sites where no White-headed Ducks were observed during repeated daytime censuses of the lake between 6 and 25 February 1993.<sup>5</sup> However, the possibility that these sites were used by ducks at night cannot be ruled out. Control sites (Fig. 1) were a freshwater inflow at the south end of the lake (SC), a bay on the northeastern shore (EC) and the inflow of the River Adalar at the northern end of the lake (NC). For behavioural studies, a 'site' was that area of the lake in which the behaviour of any White-headed Ducks could be recorded accurately from one fixed point with a telescope, whereas food supply was studied via a transect perpendicular to the shore at this point (see below).

## MATERIAL AND METHODS

### Sampling bird behaviour

Behavioural observations were carried out between 10 February and 4 March 1993, when regular surveys showed that over 2000 White-headed Ducks were present on Burdur Lake, widely dispersed around inshore areas.<sup>5</sup> Total counts peaked at 3010 but decreased towards the end of the study, probably because birds were commencing spring migration.<sup>5</sup>

Diurnal and nocturnal time budget data were collected in three-hour sessions (00.30–03.29 hours, 03.30–06.29 hours, 06.30–09.29 hours and so on, local time) alternating between one polluted and one unpolluted site in such a way that the full 24-hour cycle was covered twice at each site, totalling 192 hours of observations. MF and SW were studied from 10–18 February and SF and HB from 20 February to 4 March. Cloud-cover (%), wind speed (Beaufort scale), presence or absence of rainfall and wave-height were recorded during each 3-h observation session. Wave-height was classed as one of three categories: 'low' when birds were not obscured from view by waves, 'medium' when birds were sometimes partially obscured and 'high' when birds were sometimes wholly obscured. Three observers were



**Figure 1.** Burdur Lake, Turkey, and the sites used during the current study. Sites where White-headed Duck behaviour was sampled were a sugar factory outflow (SF), milk factory outflow (MF), a southwest bay (SW) and a holiday beach (HB). Control sites where no White-headed Ducks were recorded were an east control (EC), north control (NC) and south control (SC).

used to collect behavioural data, with two at a given site. Trials were conducted together at the start to minimize inter-observer variation.

Diurnal behaviour (06.30–18.30 hours) was quantified by instantaneous scan sampling<sup>17</sup> every 15 min from a fixed position using a ×20 wide-angle Kowa telescope, recording the behaviour of each bird on a dictaphone. Each bird was described as either adult male or female/juvenile, the latter class including juveniles of either sex, which are indistinguishable from adult females under field conditions.<sup>18</sup> Numbers of ducks recorded at the four sites were not strictly comparable, as differences in lake topography and the location of suitable observation points led to differences in length of shoreline and area of water scanned. 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 without head-on-back); *comfort* (preen, bathe, wing-flap, wing-shiver, leg-shake, stretch, yawn, head-shake and bill-dip); *swimming*; *alert* (head-up, extreme head-up and head-up–tail-up); *flying*; *social interaction* (intra- and interspecific interactions). For analysis, sleeping and loafing were combined as *resting*, while swimming and flying were combined as *locomotion*.

Nocturnal behaviour (18.30–06.30 hours) was observed using an image intensifier (Davin Optical Ltd Modulux 130) fitted with a 300 mm f2.8 lens (Tamron) and an external infra-red light source. In calm conditions, the equipment range was 400 m but this reduced to 200 m or less in poor weather; in some cases up to 150 m of this range was taken up by land between the vantage point and the lake edge. Many fewer birds were located at night due to their dispersed nature and the limited range of the night-sight, so behaviour was recorded by continuous focal sampling,<sup>17</sup> using the same categories as for daytime observations. Each study bird was observed for 30 min, or less if it swam out of sight. A different bird was then selected for observation, choosing adult males and female/juveniles alternately when possible. Behaviour was recorded using an event recorder package on a laptop computer or using a stopwatch to record the lengths of individual bouts of behaviour.

## Constructing time–activity budgets

To construct diurnal time–activity budgets, behaviour was first expressed as the mean percentage of birds engaged in each behaviour for each scan. Separate budgets were then constructed for each study site. When scanning flocks of fewer than 50 birds, the actual number of birds feeding could be recorded accurately, but some diving birds were overlooked amongst larger flocks. This source of error was corrected using two methods: (1) where bird numbers were constant and ducks moved between feeding and other activities, the number of birds overlooked was estimated from the total number of birds recorded in scans when no birds were feeding;<sup>19</sup> (2) the total number of birds feeding ( $N_i$ ) was estimated using the following equation:

$$N_i = N_i + (N_i D) / I$$

where  $N_i$  is the number of birds in inter-dive behaviour (i.e. on the surface),  $D$  is the average dive time and  $I$  is the average inter-dive interval. As we believe that  $D$  and  $I$  varied with lake depth, they were calculated separately for each site, using focal sampling data collected in between flock scans.

To construct nocturnal time–activity budgets, behaviour was first expressed as the percentage of time engaged in each behaviour for each bird sampled, excluding birds observed for less than five minutes. Means ( $\pm$  se) of time spent in each behaviour were then calculated for each study site. Too few observations were obtained from site SW for inclusion in the analysis.

## Food supply

*Oxyura* species are heavily dependent on benthic chironomid larvae.<sup>20–22</sup> At Burdur Lake, White-headed Ducks fed almost exclusively on chironomids, which constituted 99% of benthic invertebrates (there was almost no submerged vegetation in the lake).<sup>5</sup> We believe that White-headed Ducks concentrated diving at those depths that allowed an optimal foraging intake of chironomid larvae. Benthic invertebrates were sampled twice at 20-m intervals along 200-m transects perpendicular to the shore at MF, SW, SF and HB, as well as at the three control sites (Fig. 1). This allowed us to relate

the distribution and behaviour of ducks to their food supply. Each site was sampled at a different date over a 25-day period.

Benthic samples (15 cm × 15 cm) were taken from a boat using an Eckmann Grab, and water depth was recorded to the nearest 10 cm. Grab samples were washed through sieves of 1 mm and 0.25 mm mesh and all visible animals were removed and counted. Dry mass of chironomid larvae in each sample was measured after storage in 70% methanol for 1–8 days. Samples were dried on preweighed filter paper at 65°C for 72–96 hours and weighed to the nearest 0.1 mg.

### Statistical analyses

As different observation sessions at a given site were likely to include repeated observations of the same individual ducks, there was potentially a problem of non-independence. Owing to the small sample size and potential non-independence, nocturnal behavioural data were not considered sufficient for statistical analysis. To investigate differences in diurnal behaviour between polluted and unpolluted sites and the effects of weather and time-period, behavioural data were pooled for each 3-h session. Generalized linear models (GLMs) were constructed using GLIM software<sup>23</sup> with the mean percentage of birds engaged in each behaviour for each 3-h session as the dependent variable (using appropriate transformations to eliminate heteroscedasticity), with normal error and identity link functions.<sup>23</sup> Predictor variables included study site, recording period (06.30–09.29, 09.30–12.29, 12.30–15.29 or 15.30–18.29 hours) and weather parameters. Residuals in the regression models were examined to check that the data were independent between sessions. There was no evidence of serial dependence for any behaviour, with no significant correlations between a given residual in the model and the residual from the next session at the same site.

To establish the relationship between numbers of birds present and their diurnal behaviour within sites, a Pearson's correlation coefficient was calculated for each 3-h session between the numbers of birds and the percentages feeding or resting for each 15-min scan. The set of correlation coefficients was then tested for an overall deviation from zero using

a *t* test.

Factors determining benthic chironomid biomass were investigated using a GLM in GLIM with biomass as the dependent variable (log-transformed to remove heteroscedasticity), site and depth as predictors and normal error and identity link functions.

## RESULTS

### Diurnal behaviour

There was considerable daily variation in the peak numbers of White-headed Ducks recorded at the four study sites during sampling of diurnal behaviour (MF: mean ± sd = 28.2 ± 18.0, *n* = 6; HB: mean = 37.9 ± 27.8, *n* = 9; SW: mean = 110.9 ± 69.2, *n* = 7; SF: mean = 313.6 ± 114.9, *n* = 7). Any migration away from the lake had no noticeable influence on numbers at any site (there was no significant correlation between duck numbers and date at any study site, Spearman rank correlations, *P* > 0.1 ns).

Feeding, resting and locomotion were the dominant diurnal behaviours, together constituting over 93% of all activity at each site (Table 1). The only other behaviours which were regularly recorded were comfort and alert. Alert behaviour was usually adopted in the presence of predatory gulls.<sup>24</sup>

Time-activity budgets suggested marked differences between sites (Table 1). Birds spent more time feeding and moving at MF and HB and more time resting at SF and SW. There were marked differences in diurnal rhythms of activity at each site (Fig. 2). At SW, there was a clear peak in resting and a trough in feeding during the middle of the day, with troughs in resting and peaks in feeding around dawn and dusk. No such clear pattern was discernible at the other sites (Fig. 2).

GLMs confirmed that there were highly significant differences between sites and time-periods in the amount of time spent feeding and resting (Table 2). Weakly significant interactions were found between site and time-period for feeding ( $F_{9,12} = 3.78$ , *P* < 0.05) and resting ( $F_{9,12} = 2.98$ , *P* < 0.05), showing that the effect of time differed between sites (Fig. 2). There was also a highly significant effect of wave-height on behaviour, with birds consistently resting less and moving and feeding more as wave-height increased (Table 2). The

**Table 1.** Diurnal (06.30–18.29 hours) and nocturnal (18.30–06.15 hours) time–activity budgets of White-headed Ducks at different study sites.

Behaviour	Sugar factory		Milk factory		Southwest bay	Holiday beach		Total	
	Day n = 97	Night n = 12.1 <sup>23</sup>	Day n = 80	Night n = 6.4 <sup>17</sup>	Day n = 92	Day n = 100	Night n = 5.9 <sup>14</sup>	Day n = 369	Night n = 24.4 <sup>54</sup>
Feeding	13.9 ± 1.6	87.3 ± 6.3	35.6 ± 3.4	92.5 ± 5.9	19.3 ± 2.3	42.9 ± 3.1	99.7 ± 0.6	27.8 ± 1.5	92.2 ± 3.4
Resting	76.8 ± 2.5	9.5 ± 6.1	41.0 ± 3.9	0	67.1 ± 3.1	40.8 ± 3.3	0	56.9 ± 1.8	4.1 ± 2.7
Locomotion	3.7 ± 0.8	1.8 ± 1.3	17.3 ± 3.0	7.5 ± 5.9	9.7 ± 1.5	12.7 ± 2.4	0.3 ± 0.2	10.6 ± 1.0	3.2 ± 1.9
Comfort	3.6 ± 0.8	1.4 ± 1.3	4.1 ± 1.3	< 0.1	3.5 ± 0.6	3.4 ± 0.6	< 0.1	3.7 ± 0.4	0.6 ± 0.5
Alert	2.0 ± 1.4	0	2.0 ± 1.4	0	0.4 ± 0.2	0	0	1.1 ± 0.5	0

Means ( $\pm$  se) are presented for percentage time in each behaviour; *n* for diurnal data is number of scans, *n* for nocturnal data is number of hours of focal data, with number of birds observed in superscript. Resting includes sleeping (52.6% by day, 3.3% by night) and loafing (4.3% by day, 0.8% by night). Locomotion includes swimming (10.2% by day, 3.2% by night) and flying (0.4% by day). No sexual behaviour was observed, and only one intraspecific interaction (a threat display) was observed, constituting 0.02% of diurnal activity.

effect of wave-height remained significant when the interaction between site and time was included in the models. Wind-speed, rainfall and cloud-cover were also significantly correlated with some behaviours. However, these

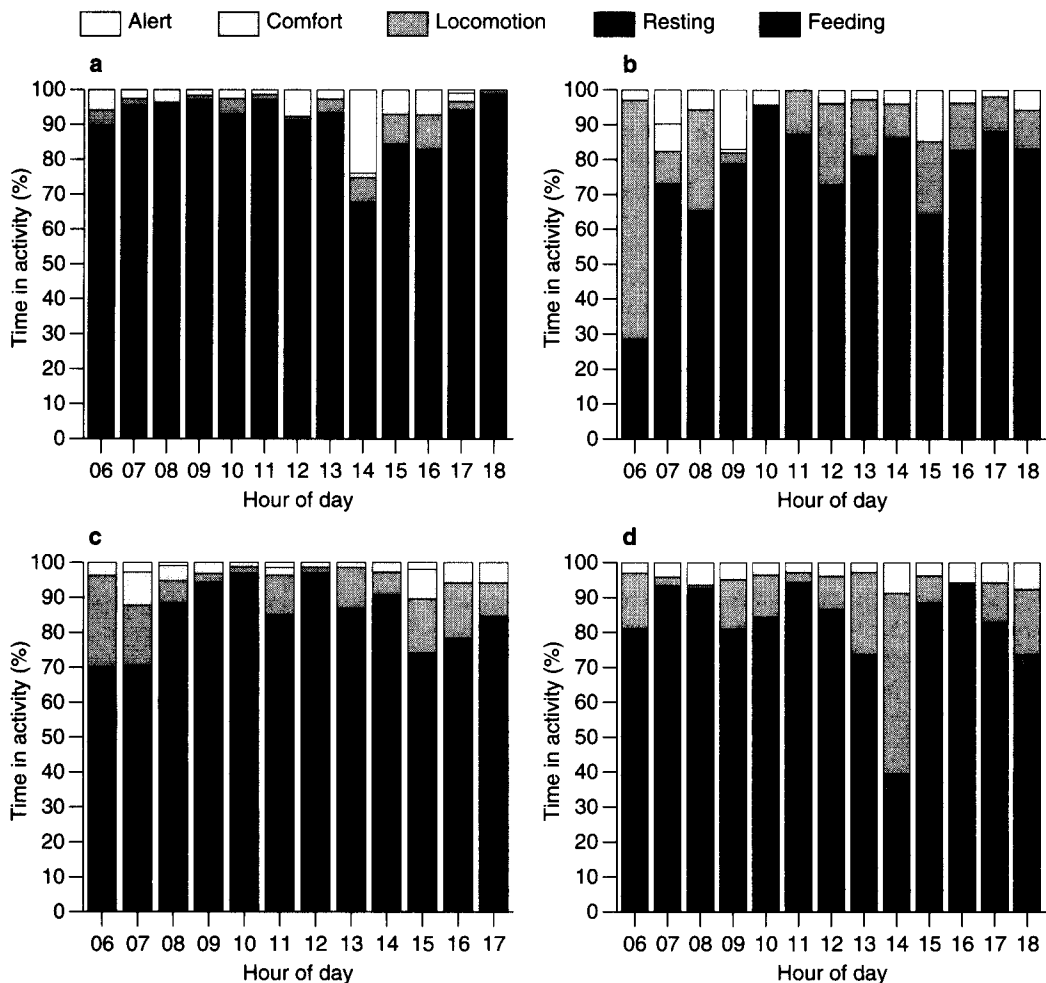
variables were highly correlated with wave-height and when they were included together in the GLM, only the partial effects of wave-height remained significant. Wave-height explained more variance than any other weath-

**Table 2.** GLM models of diurnal behaviour of White-headed Ducks, with percentage of birds in each behaviour (averaged for each 3-h session) as dependent variable, showing the parameter estimates (PE) and their standard errors.

	Feeding			Resting			Locomotion		
	PE	se	F-ratio	PE	se	F-ratio	PE	se	F-ratio
Constant	28.61	2.430		40.91	7.879		17.35	1.391	
Site									
SF	0.029	2.766	10.09***	14.25	8.967	6.34**	-4.426	1.583	2.89
MF	10.73	2.924		-17.72	9.479		-1.325	1.674	
HB	9.62	2.450		-16.20	7.943		-1.318	1.403	
Wave height									
Medium	10.18	2.824	14.35***	-22.82	9.155	13.22***	0.890	1.617	8.61***
High	11.52	2.494		-39.73	8.084		5.906	1.428	
Time									
09.30–12.29	-12.15	2.745	9.47***	31.87	8.899	4.98**	-1.772	1.571	1.76
12.30–15.29	-11.67	2.741		19.65	8.885		1.567	1.569	
15.30–18.29	-4.54	2.744		8.999	8.896		-0.222	1.571	
Residual									
deviance	49.58		10.58***	5211		7.67***	16.249		3.86**
df	21			21			21		

Dependent variables were transformed as  $10(\log_e[\%feeding])$ ,  $(\%resting)^2/100$  and  $10(\%locomotion)^{0.5}$ . Site SW, wave-height low and time 06.30–09.29 were aliased. F-ratios are presented for the partial effects of study site (factor of four levels), time-period (factor of four levels) and wave-height (factor of three levels), and for the whole regression.

\*\**P* < 0.01; \*\*\**P* < 0.001.



**Figure 2.** Diurnal rhythms of White-headed Ducks for study sites (a) SF, sugar factory, (b) MF, milk factory, (c) SW, southwest bay and (d) HB, holiday beach, plotted from hourly means of the percentage of birds in each scan engaged in each behaviour.

er parameter, and the partial effect of wave-height in the GLMs of Table 2 explained 27%, 32% and 33% of the total variation in feeding, resting and locomotion behaviour, respectively.

Date and date<sup>2</sup> were included as predictor variables in the GLMs of behaviour, and had no significant effects. Time-activity budgets for adult males and female/juveniles were almost identical, with no significant differences in the percentage of feeding, resting or in locomotion (*t* tests comparing matched pairs for each observation session,  $P > 0.3$  ns).

While controlling for site differences and

wave-height in GLMs, time-periods were ranked 06.30–09.29 > 15.30–18.29 > 12.30–15.29 > 09.30–12.29 hours for percentage feeding and the reverse for percentage resting (Table 2). Thus, feeding peaked around early morning and late afternoon periods and resting peaked in the middle of the day. While controlling for time-period and wave-height in GLMs, the study sites were ranked MF > HB > SF > SW for percentage feeding and SF > SW > HB > MF for percentage resting (Table 2).

There were no consistent differences in behaviour between polluted (MF and SF) and unpolluted (HB and SW) sites. However, birds

rested more and fed less at those sites (SF and SW) which held more birds. Similarly, there was a significant relationship within sites between the number of birds present and the proportion of time spent feeding and resting. For each 3-h observation session (pooling all sites), the proportion of birds feeding and resting in each scan was correlated with the number of birds scanned. The number of birds was correlated positively with the proportion of birds resting (mean  $r \pm sd = 0.313 \pm 0.365$ ,  $n = 32$ ,  $t_{31} = 4.84$ ,  $P < 0.0001$ ), and negatively with the proportion feeding (mean  $r \pm sd = -0.257 \pm 0.310$ ,  $t_{31} = -3.87$ ,  $P < 0.001$ ). These trends were consistent at each site and statistically significant at all except MF.

### Nocturnal behaviour

Owing to the limitations of the equipment and methods used, only 24.6 h of focal data from 54 individual ducks were obtained from 84 h of nocturnal observations. White-headed Ducks spent 92% of their time feeding at night, with less variation between sites than during the day (Table 1). Feeding was observed at all phases of the moon. Large, resting flocks regularly observed within nightscope range during the day were never seen at night. Birds rested more at SF (9.5%) than at MF and HB, as found during the day (Table 1). Time spent in comfort was probably underestimated slightly because some short bouts of preening during inter-dive behaviour could not be identified owing to poor visibility.

### Food supply

The mean and maximum biomass of benthic chironomids varied between sites (Table 3). Both means and maxima were significantly higher at the four study sites with White-headed Ducks than at the three control sites without them (two-tailed two-sample  $t$  tests, means:  $t_5 = 2.70$ ,  $P < 0.05$ ; maxima:  $t_5 = 4.00$ ,  $P = 0.01$ ). However, the variation between the sites in percentage diurnal time spent feeding by White-headed Ducks (Table 1) was not related to gross differences in chironomid biomass (Table 3).

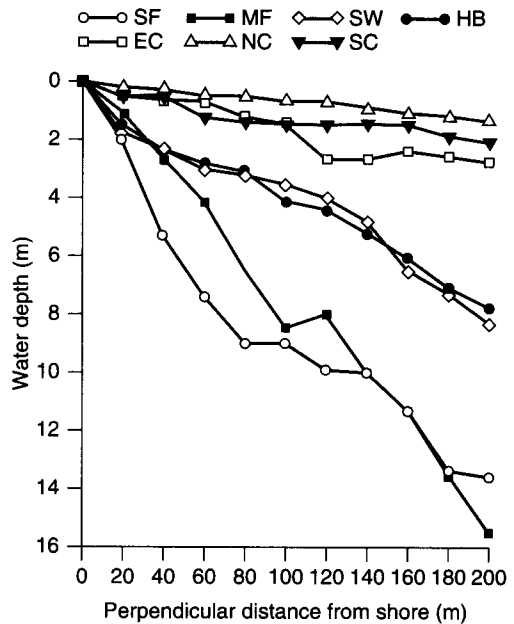
A GLM showed that there were highly significant effects of depth and site on chironomid biomass (Table 4). Biomass gradually

**Table 3.** Summary of chironomid larval biomass ( $\text{g}/\text{m}^2$ ) at sites with and without White-headed Ducks (based upon 20 grab samples along a 200-m transect at each site).

Site	Mean biomass	Standard error of mean	Maximum biomass
Sugar factory	1.156	0.152	2.222
Milk factory	1.462	0.277	3.356
Southwest bay	0.564	0.204	2.511
Holiday beach	0.636	0.149	1.991
East control <sup>a</sup>	0.375	0.081	1.280
North control <sup>a</sup>	0.293	0.041	0.667
South control <sup>a</sup>	0.002	0.001	0.014

<sup>a</sup>Site where White-headed Ducks were never recorded.

increased from depth zero, peaked at a depth of around 10 m and then declined again at greater depths.<sup>25</sup> Differences in mean chironomid biomass between sites (Table 3) were largely explained by the differences in depth profiles (Fig. 3). Sites where White-headed Ducks were absent were too shallow to support a



**Figure 3.** Water depth profiles from the four study sites occupied by White-headed Duck (SF, MF, SW and HB) and from three control sites where they were absent (EC, NC and SC).

**Table 4.** GLM model of biomass of benthic chironomids.

	Parameter estimate	Standard error	F ratio
Constant	-5.809	5.279	
Site			
SF	-6.307	4.770	44.2***
MF	3.753	4.638	
SW	-17.16	4.231	
EC	28.98	4.796	
NC	47.97	5.395	
SC	-11.21	4.965	
Depth	17.32	1.438	145.1***
Depth <sup>2</sup>	-0.865	0.09378	85.1***
Residual deviance	2345		60.4***
df	131		

Dependent variable was biomass transformed as  $10(\log_e([\text{mg m}^{-2}] + 1))$ . F-ratios are presented for the predictor variables depth, depth<sup>2</sup> and site (factor of seven levels), and for the whole regression. Site HB was aliased. Interaction terms added to this model (site  $\times$  depth + site  $\times$  depth<sup>2</sup>) had a highly significant effect ( $F_{12,119} = 7.13^{***}$ ).

\*\*\* $P < 0.001$ .

considerable biomass (Fig. 3).

There were major differences between sites in chironomid biomass at a given depth (Table 4). According to the parameter estimates from the GLM of Table 4, the rank order of biomass for a given depth is MF > HB > SF > SW. This is the same rank order of sites for percentage feeding by ducks according to the parameter estimates of the GLM in Table 2, and the estimates for each site from the two models are closely correlated ( $r_2 = 0.87$ , ns). Thus, birds fed more during daytime at sites with a higher chironomid biomass for a given depth.

## DISCUSSION

### Site selection

The distribution of ducks around the lake was related to the distribution of chironomids, with ducks absent from areas with a low chironomid biomass. White-headed Ducks were not found at sites with a maximum biomass of less than 1.5 g/m<sup>2</sup> of chironomids, roughly equivalent to densities of fewer than 15 000 chironomids per

m<sup>2</sup>. We cannot rule out the possibility that White-headed Ducks or other ducks had already depleted chironomid numbers in these parts of the lake earlier in the winter. Wintering Pochard *Aythya ferina* have also been shown to select foraging sites supporting higher than average numbers and biomass of chironomid larvae.<sup>12</sup> In both this study and that of Phillips,<sup>12</sup> chironomid biomass was strongly correlated with water depth, and it is unclear whether ducks were distributing themselves in relation to depth or chironomid biomass *per se*.

Individual White-headed Ducks made regular movements from one part of the lake to another. This led to considerable variation in the number of birds present at each study site between days, and even between 15-min scans. Individuals were regularly observed swimming into and out of study sites. Birds were also seen flying to and from sites, particularly when attacked by gulls.<sup>24</sup> Those movements not caused by gull attacks were mainly associated with a switch in activity between feeding and resting. White-headed Ducks concentrated together into densely packed flocks when resting, but dispersed widely when feeding.<sup>24</sup> This explains the correlations within and between sites between the number of birds and the proportions resting and feeding.

Flocking when resting reduces individual risk of gull predation.<sup>24</sup> Foraging birds presumably disperse away from flocks in order to forage at locations that allow a greater food intake. Decisions as to which sites to use for resting or feeding probably depend on a combination of factors, including food supply, predation risk and thermoregulatory costs.<sup>26,27</sup> Travel costs will influence distances moved between sites when switching activities. Sites MF and HB were used relatively more for feeding, perhaps because the chironomid biomass at a given depth (and thus foraging intake)<sup>28</sup> were highest at these sites. Sites SF and SW were used relatively more for resting, perhaps because they provided better shelter from rough weather and/or predators. SF consists of an almost enclosed bay, providing particularly good shelter from prevailing winds. Owing to reduced fetch (i.e. upwind distance to the bank), wave-height and thus energetic costs to ducks were probably lower at SF.<sup>16</sup> MF was a major roost site for predatory

gulls, which may explain why it was used by relatively few ducks which spent little time resting.

### Diurnal time–activity budgets

Resting was the dominant diurnal activity at all study sites. Amat<sup>10</sup> found that White-headed Ducks wintering in Spain had a similarly low level of daytime feeding. The lack of courtship activity during the current study is typical of wintering stiff-tails and consistent with the polygamous mating system of White-headed Ducks, in which males establish and court within territories at breeding sites.<sup>29,30</sup>

Diurnal time budgets showed significant differences between different parts of Burdur Lake. GLM analysis showed that percentage feeding was higher at sites with higher chironomid biomass at a given depth. Although this was not statistically significant, it provides the most likely explanation for the differences in time budgets between sites, with birds moving around and feeding most in sites allowing a higher foraging intake. If birds were static, the opposite would be expected, i.e. they would spend more time feeding at sites with poorer foraging conditions.

Although not all study sites were sampled on the same dates, there was no evidence of seasonal effects on time budgets. Date had no effect on activity, and sites that had similar levels of feeding and resting (e.g. MF and HB) were sampled at different dates. Our study illustrates the importance of sampling water-bird behaviour at as many places as possible, because different parts of a wetland complex may be used for different behaviours.<sup>15,31–33</sup> However, many previous time–activity studies of ducks have only sampled one site, and their results may therefore be heavily biased towards certain behaviours.<sup>19</sup>

We found that diurnal feeding peaked in the early morning and late afternoon, as found in several other wintering duck species<sup>8,16</sup> (but see Hepp<sup>34</sup>). This has been attributed to the inability of birds feeding mainly nocturnally to meet their nutritional needs at night alone.<sup>16</sup> Digestive bottlenecks may limit how much time birds spend feeding at night,<sup>35</sup> although this requires further study. This pattern may also be explained by a thermoregulatory advantage to resting in the middle of the day,

when surface temperatures are highest (see below). We also found a site–time interaction, showing that diurnal rhythms of feeding and resting varied between sites, possibly due to the movement of birds between sites when they switch activities.

### Nocturnal time–activity budgets

White-headed Ducks at Burdur Lake spent much more time feeding at night (92%) than during the day (28%). Although behaviour was sampled using different methods by day and night, this cannot explain such different results. As nocturnal time budgets were heavily biased towards birds closest to the shore, it is possible that the amount of time spent resting, and differences between sites, were underestimated at night. Nevertheless, resting flocks seen within intensifier range during the day were not there at night.

Potential reasons why White-headed Ducks feed mainly at night include lack of disturbance, avoidance of diurnal predators, thermoregulation and increased food availability.<sup>7–9,31</sup> Although illegal hunting occurs at Burdur Lake, the resulting disturbance is not a plausible explanation for the nocturnal activity of White-headed Ducks, because hunting evoked almost no escape response from these birds.<sup>5</sup> In contrast, day-active predatory gulls exerted a strong influence on White-headed Duck behaviour.<sup>24</sup> Feeding ducks were more isolated from conspecifics and hence more at risk from gulls. Although nocturnal foraging may thus have reduced predation risk in the current study, Amat<sup>10</sup> found similar low levels of diurnal feeding by White-headed Ducks in the absence of predators and with little human disturbance. Wintering Ruddy Ducks feed mainly at night in the absence of diurnal disturbance.<sup>36,37</sup>

Nocturnal feeding may have provided the White-headed Ducks with thermoregulatory benefits through the concentration of heat-generating foraging activity in nocturnal periods of lowest temperatures (sub-zero air temperatures were common at night), and the opportunity to sunbathe while resting during the day.<sup>7–9</sup> It is also possible that White-headed Ducks fed nocturnally to increase their foraging intake. Benthic chironomids move up within the substrate at night,<sup>38</sup> concentrating

potential prey at or around the lake bed. This may also explain nocturnal foraging in Ruddy Ducks,<sup>37</sup> which also feed largely on chironomid larvae.<sup>22</sup>

### Influence of weather

The observed increase in feeding and swimming and decrease in resting with increasing wave-height could be explained in several ways. Higher waves increase energetic demands on ducks and hence their need to spend time feeding. It is possible that foraging intake is reduced in such conditions, further increasing the time that ducks need to spend feeding. The thermoregulatory benefits of daytime resting may be eliminated in rough weather, because resting postures may offer high wind resistance and skies are usually overcast, preventing sunbathing. White-headed Ducks at the surface faced into high winds with their heads held low so as to minimize resistance to wind and waves. Furthermore, the relative energetic cost of diving may be reduced if the currents associated with waves are strongest at the lake surface. Alternatively, there may be a lower risk of predation by gulls in higher waves, since it is probably harder for a gull to pursue individual ducks.<sup>24</sup> Gulls seemed less likely to attack White-headed Ducks as wave-height increased during the current study.

Variable responses of waterfowl to severe winter weather have been recorded previously.<sup>8,32-34,39</sup> Michot *et al.*<sup>16</sup> found Redheads *Aythya americana* to increase feeding with increased wind-speed and wave-height and colder temperatures, and attributed this to higher thermoregulatory demands. Ducks sometimes reduce the effects of severe weather on energy demands by resting in thermally favourable microhabitats.<sup>40,41</sup>

The availability of such habitats helps to explain the contrasting results of different studies. Burdur Lake offers White-headed Ducks little shelter from high winds owing to a lack of emergent vegetation, and birds sometimes drown during storms.<sup>42</sup> Thus, heat loss cannot be reduced significantly by resting. In contrast, Ruddy Ducks spend less time feeding in high winds at wetlands with fringes of emergent vegetation that allow them to shelter out of the wind.<sup>37</sup>

### Conclusions

White-headed Ducks wintering at Burdur Lake are largely nocturnal and highly mobile, typically moving hundreds of metres when switching between resting (in flocks to reduce predation risk)<sup>24</sup> and feeding. Their distribution, particularly when feeding, is strongly dependent on the distribution of their food supply, benthic chironomid larvae. Burdur Lake offers little shelter against harsh weather conditions, which have a marked effect on duck behaviour. The availability of relatively sheltered bays on the lake (e.g. at SF) is probably vital to reduce duck mortality in winter. The results of this study are consistent with the hypothesis that numbers of White-headed Ducks wintering at Burdur Lake are partly limited by the abundance of benthic chironomids, and that a reduction in their food supply is one factor explaining the current decline in duck numbers.<sup>6</sup> Ongoing declines in lake depth and size, together with sedimentation, are likely to be reducing the biomass of chironomids in the lake.<sup>5</sup> This may explain why, in February 1991, 4000 White-headed Ducks were recorded in the northern part of the lake,<sup>43</sup> whereas in 1993 they were absent from this area where food supply was very low. Our study provides no evidence that organic pollution entering the lake at SF and MF<sup>5</sup> poses a short-term threat to the White-headed Ducks. Further research is required to relate seasonal and annual variation in chironomid abundance to changing numbers and distribution of waterbirds at Burdur Lake, as well as to assess the impacts of a new airport and industrial development on the northern shore.<sup>5</sup>

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