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SLEEP-VIGILANCE TRADE-OFF IN GADWALL DURING THE WINTER PERIOD[1]

MICHEL GAUTHIER-CLERC[2] AND ALAIN TAMISIER
Centre d'Écologie Fonctionnelle et Évolutive—CNRS, Route de Mende, 34000 Montpellier, France

FRANK CÉZILLY
Université de Bourgogne, Laboratoire Écologie-Évolution, 6 Boulevard Gabriel, 21000 Dijon, France

Abstract. We studied vigilance while sleeping in wintering Gadwalls (*Anas strepera*) in the Camargue (southern France) during the 1992–1993 and 1994–1995 winters. Vigilance while sleeping was reduced at the beginning and at the end of the winter. During mid-winter, birds in sleeping posture showed the highest level of vigilance, with longer peeks and shorter interpeek intervals. There was no effect of sex on the intensity of vigilant sleep, nor on changes in the pattern of vigilant sleep across the winter period. We discuss the results in relation to the behavioral ecology and energetic constraints of wintering Gadwalls in the Camargue. We suggest that the variation in sleep, measured by eye-closure, and vigilance, measured by eye-opening, in relation to winter period is a result of a trade-off between two opposite requirements: to save energy by sleeping and to monitor the environment by being vigilant.

Key words: Anas strepera, *Camargue, Gadwall, sleep, vigilance, wintering strategies.*

INTRODUCTION

Sleeping animals may be more exposed to external danger if sleep and vigilance are mutually exclusive (Allison and Van Twyver 1970, Lendrem 1983). To solve this dilemma, sleeping birds alternate periods of eye closure with short periods of eye-opening, referred to as "peeks" (Lendrem 1983) or vigilant sleep (Amlaner and Ball 1994). Thus despite being in a sleeping posture, during vigilant sleep birds may scan their surrounding environment (Amlaner and Ball 1994). In addition, vigilant sleep may allow sleep processes to continue or start again with minimal interruption (Amlaner and Ball 1994). Vigilant sleep has been studied as an analogue to the scanning behavior of foraging birds (Lendrem 1983, Gauthier-Clerc et al. 1994).

Electrophysiological studies have confirmed that eye state (open or closed) can be used to assess sleep in birds (Amlaner et al. 1985, Ayala-Guerrero et al. 1988, Szymczak et al. 1993). When the eyes are closed, EEG traces exhibit activity characteristic of quiet or active sleep (states analogous to mammalian slow-wave or non-rapid eye movement sleep and paradoxical or rapid eye movement sleep, respectively), whereas waking patterns are exhibited when the eyes are open. During peeks, the electrophysiological evidence indicates an intermediate status between quiet sleep and relaxed wakefulness (Amlaner et al. 1985). Thus, eyelid closure can be used in the field as a behavioral measure of sleep, with shorter and less frequent peeks indicating more sleep (Amlaner et al. 1985, Amlaner and Ball 1994).

Sleep may be partly seen as an energy-saving process (Allison and Van Twyver 1970, Berger and Phillips 1995), whereas vigilance is an important feature in the detection of external danger or environmental resources, and in intraspecific communication (Dimond and Lazarus 1974). As the time spent peeking occurs at the expense of eye closure, the problem facing a bird is how best to allocate its time between these conflicting demands (Lendrem 1983). Although the investigation of the adaptive value of vigilant sleep is essential to assess its advantageous and deleterious consequences, the ecological and physiological factors affecting the trade-off between sleep and vigilance in free-ranging birds remains largely unknown.

Ducks typically engage in vigilant sleep while roosting during the day (Amlaner and Ball 1983, Lendrem 1983). In the Camargue (Rhone Delta, southern France), the seasonal variation in energetic constraints and behavioral ecology has

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[2] Current address: Centre d'Écologie et Physiologie Énergétiques—CNRS, 23, rue Becquerel, 67087 Strasbourg cedex 2, France, e-mail: michel.gauthier-clerc@c-strasbourg.fr

been documented for wintering ducks (Tamisier et al. 1995, Tamisier and Dehorter 1999). In this area, ducks face important energetic constraints at the beginning (September and October) and the end (from late January to March) of the winter period. At the beginning of the winter period, ducks have to recover from severe energy expenses associated with molt and migration (Tamisier et al. 1995). At the end of winter, ducks face important energy requirements in relation to imminent return migration and reproduction, whereas food availability decreases, climatic conditions are colder, and their body mass declines until March (Fox et al. 1992, Tamisier et al. 1995). In contrast, in mid-winter, energetic constraints are lower, but predator pressure is higher. At this time, ducks show the highest body reserves, more than 30% compared to the beginning of winter, and engage in courtship and pairing activities (Allouche and Tamisier 1989, Tamisier et al. 1995).

In a previous study, we found that vigilance levels while sleeping (measured by peek frequency) decreased at the end of winter in Green-Winged Teal (*Anas crecca,* Gauthier-Clerc et al. 1998). We investigate in the present study variations of vigilant sleep during the winter period in another species, the Gadwall (*Anas strepera*), wintering in the same area. Compared to Green-Winged Teals, Gadwalls present a reduced sexual dimorphism in plumage, with no bright color and only a slight difference between eclipse and nuptial plumage. This feature rules out the possible cost of a colorful plumage, which may induce higher predation pressure (Lendrem 1983). Moreover, we include the beginning of the winter period and control the effect of other potential variables which might affect the results, such as group size, distance from shore and predator presence.

The objective of the present study was to determine whether patterns of vigilant sleep in Gadwalls are adjusted to energetic and ecological constraints during the winter period. The hypothesis is that at the beginning and at the end of the winter period, when energetic constraints are the highest, sleep, measured by eye-closure, serves an energy conservation function and acquires a higher priority at the expense of vigilance.

METHODS

SUBJECTS AND STUDY SITE

Gadwall is a medium-sized dabbling duck, with a slight sex-related dimorphism in plumage color (Cramp and Simmons 1977). Gadwall are vegetarian, feeding essentially on *Potamogeton pectinatus,* a low energetic food, in fresh and semi-permanent waters (Allouche and Tamisier 1989). The Camargue is a main wintering area in Europe for this species. Birds wintering in Camargue breed in central and north Europe (up to Sweden). As the flight distances involved may be over several thousand kilometers, the energetic requirements of migration are important.

Gadwall were observed on the Saint-Seren, a 70-ha freshwater marsh situated in the estate of the Station Biologique de la Tour du Valat. This marsh is one of the major roosting sites for ducks in the Camargue, with about 36,000 wintering ducks, of which 5,000 are Gadwalls (Tamisier and Dehorter 1999). Wintering Gadwalls roost communally during the day with other duck species, including Red-crested Pochard (*Netta rufina*), Shoveler (*Anas clypeata*), Mallard (*Anas platyrhynchos*), and Green-winged Teal. Gadwall mostly sleep and perform comfort activities (60% of the diurnal time) and feed less frequently (25% of the diurnal time) (Allouche and Tamisier 1989). Most foraging activity takes place at night in other marshes with higher food availability (Tamisier 1970, Allouche 1988).

DATA COLLECTION

Observations were made from a hide, using a 20× telescope. During days of observations, weather conditions were good, without rainfall and with similar wind speed. We avoided highly windy days which induced drift of the ducks sleeping on water and thus increased the vigilance level (pers. observ.). Ambient temperature during days of observations decreased from 20°C in September to 11°C in November and varied between 5 and 10°C between December and March.

Gadwall mostly sleep with head on the back and bill under scapulars. They may sleep with head facing forward. However, we observed this sleeping posture only during very warm periods of the day in September, probably in relation to thermoregulation, and in this case in only 9% of the birds. Consequently, we did not include this sleeping posture in the analysis. Birds were randomly selected in large, dense groups of at least 300 ducks to avoid group-size effects, as already reported (Lendrem 1983, Gauthier-Clerc et al. 1998).

Sleeping ducks typically show brief and frequent peeks. However, although being in sleeping posture, they can maintain an open eye for longer period. Moreover, in risky situations, ducks can sleep with one eye open and one hemisphere of the brain awake, so called unihemispheric sleep (Ball et al. 1985, Rattenborg et al. 1999). As the eyes of ducks are located laterally, we observed only one eye at a time and, thus, we did not study unihemispheric sleep. We assume it did not influence our results because through the winter birds were not selected in the edge of flocks and were observed sleeping in the same area and from the same hide. Moreover, left or right eye was randomly selected. We assume that our random sample does not include significant replication, because several thousands of Gadwall may be sleeping simultaneously in this marsh, and thus the same bird was unlikely to have been observed more than once.

In the winter 1992–1993, we used the same method as in our Green-Winged Teal study (Gauthier-Clerc et al. 1998), recording the absolute frequency of peeks, only during periods when these peeks were brief, lasting approximately less than 1 sec, to avoid bias in peeking rate due to scan duration. We observed birds from dawn to dusk during two days or three days each month from September to January.

From September 1994 to March 1995, we collected behavioral data each month (except in January) during the morning of two consecutive days. Firstly, time budgets of roosting birds were collected, through recordings of randomly selected individuals. Whether active or in a sleeping posture was recorded for each individual by instantaneous sampling (Martin and Bateson 1986). Secondly, the focal sampling technique (Martin and Bateson 1986) was used to obtain an accurate description of the vigilant behavior of birds in sleeping posture. Observations lasted for 2 min. Using a tape recorder and a stopwatch, we recorded the absolute frequency of peeks, and the duration of consecutive peeks and interpeek intervals (± 0.3 sec). Focal individuals, all in sleeping posture, were classified in four categories according to the percentage of time spent with eyes opened (Table 1).

DATA ANALYSIS

Data on categorical variables were analyzed with nonparametric statistics (Siegel and Castellan 1988), whereas the effect of sex and date (month) on the variables measured on a ratio scale were analyzed with two-way ANOVAs with unequal sample size (Snedecor and Cochran 1980). Arcsine and logarithmic transformations (Sokal and Rohlf 1981) were performed, respectively on percentage of time spent vigilant per observation, and on duration of peeks and interpeek intervals, in order to obtain normal distributions. All tests were two-tailed. Results were considered to be significant at the 5% level. Means are reported ± SD.

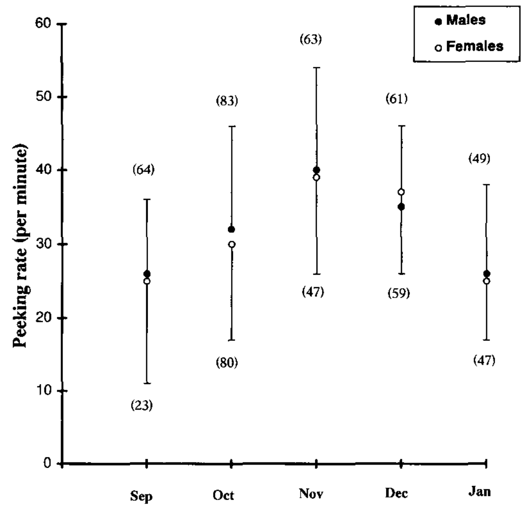

FIGURE 1. Means values of peeking rate in male and female Gadwalls from September to January 1993. Vertical bars show standard deviation. Sample size in parentheses.

RESULTS

In the winter 1992–1993, the data set consisted of 320 focal observations of males and 256 of females. Mean duration of a focal observation was not different between males and females (mean duration 34 and 35 sec for males and females, respectively, $F_{1,574} = 0.4$, $P > 0.5$). Peeking rates ranged from 3 to 70 peeks min^{-1}, with a mean rate of 32 ± 12 peeks min^{-1} and 32 ± 13 peeks min^{-1} for males and females, respectively. Peeking rates significantly differed between months ($F_{4,571} = 36.0$, $P < 0.001$), whereas there was no effect of sex or sex-by-month interaction. Peeking rate increased from September to November and decreased afterwards (Fig. 1).

In the winter 1994–1995, the percentage of Gadwall in sleeping posture differed significantly between months (Table 1, $\chi^2_5 = 183.3$, $P <$

TABLE 1. Absolute frequencies of Gadwalls among focal individuals in sleeping posture according to the time spent with eyes open, and percentage of individuals in sleeping posture for each month during winter 1994–1995.

Time spent with eye open	Sep	Oct	Nov	Dec	Feb	Mar
Category 1 ("sleeping" bird): <5%	0	0	0	0	1	1
Category 2 ("sleeping" bird): <50%	21	42	42	54	58	68
Category 3 ("awake" bird): ≥50%	5	10	31	28	4	14
Category 4 ("awake" bird): ≥95%	0	0	7	4	1	0
n	26	52	80	86	64	83
Proportion of Gadwalls in sleeping posture (%)	50	48	53	79	81	86
n	1,086	352	428	144	247	170

0.001), increasing regularly from September to March (Table 1). From 391 focal observations (201 males and 190 females), the proportions of birds in the four categories differed significantly between months (Table 1, $\chi^2_5 = 40.6$, $P < 0.001$). We pooled data from category 1 and 2 ("sleeping" birds) and data from category 3 and 4 ("awake" birds). There was no significant difference in the proportions of sleeping and awake birds between September and October ($\chi^2_1 = 0.01$, $P > 0.7$), between November and December ($\chi^2_1 = 1.4$, $P > 0.2$), or February and March ($\chi^2_1 = 1.9$, $P > 0.1$). Pooling data between two consecutive months, the proportions of sleeping and awake birds in November–December differed significantly from the ones in September–October ($\chi^2_1 = 11.4$, $P = 0.001$) and those in February–March ($\chi^2_1 = 31.3$, $P < 0.001$), whereas there was no significant difference between the two latter periods ($\chi^2_1 = 1.1$, $P > 0.2$). The proportion of awake birds varied from 80% at the beginning and end of the winter to 50% during mid-winter. The duration of peeks ranged from 0.3 to 15 sec (median = 1 sec), whereas the duration of interpeek intervals ranged from 0.3 to 11.3 sec (median = 1.3 sec). For all three variables, percentage of time spent with eye open, duration of peeks, and duration of interpeek intervals, mean values differed significantly between months ($F_{1,5} = 20.7$, $P < 0.001$; $F_{1,5} = 11.9$, $P < 0.001$; $F_{1,5} = 15.8$, $P < 0.001$, respectively), whereas there was no effect of sex or sex-by-month interaction ($F_{2,4} = 2.4$, $P > 0.1$; $F_{2,4} = 2.1$, $P > 0.1$; $F_{2,4} = 2.3$, $P > 0.1$, respectively) (Fig. 2 and 3). November and December corresponded to the peak period for intensity of vigilance with the highest values of percentage of time spent vigilant and of duration of peeks

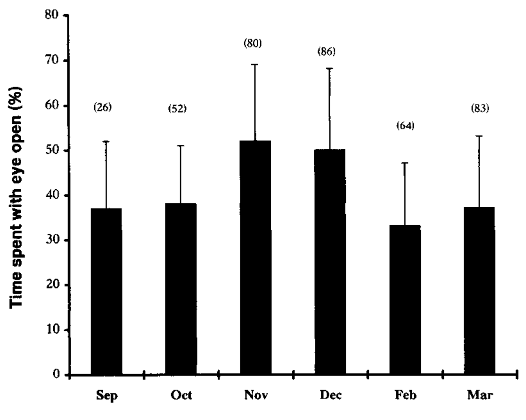

FIGURE 2. Variation between months in the proportion of time spent with eye open per focal observation during winter 1994–1995. Vertical bars show standard deviation. Sample size in parentheses.

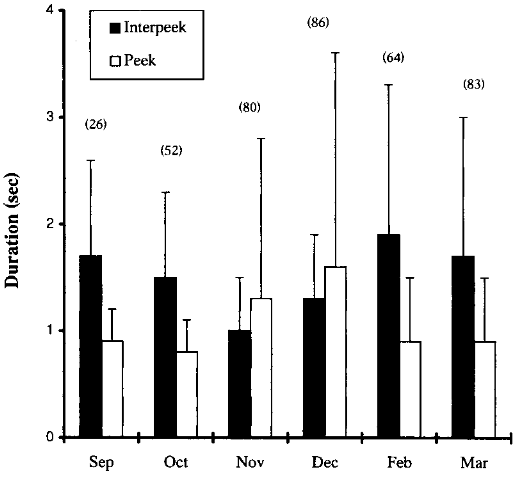

FIGURE 3. Variation between months in the mean values of the duration of peeks and interpeek intervals during winter 1994–1995. Vertical bars show standard deviation. Sample size in parentheses.

and the lowest values of duration of interpeek intervals.

DISCUSSION

We found similar monthly changes in the pattern of vigilant sleep in Gadwall during two different winters, with an increase in sleep early and late in winter. There was no effect of sex on the intensity of vigilant sleep.

Previous studies of sleeping ducks found sex-related differences in vigilance levels (Lendrem 1983, Gauthier-Clerc et al. 1998). Similarly, Mayhew (1987) reported that male European Wigeons (*Anas penelope*) are more vigilant than females during foraging. It was suggested that males of dimorphic species experience a higher predation pressure due to their colorful nuptial plumage, and therefore are more vigilant (Lendrem 1983). Conversely, according to the present study, males and females in sleeping posture spend equal proportions of time scanning the environment and showed similar variation of sleep patterns through the winter period. However, because Gadwalls show limited sexual dimorphism in plumage color, this result remains consistent with previous interpretations of patterns of vigilance in ducks. Additional information on sex-related vigilant behavior in duck species with various degrees of sexual dimorphism would help assess the precise cost of nuptial coloration in males.

The detailed analysis of vigilant sleep shows that the sleeping posture is not a reliable index of the intensity of sleep, as already shown by Amlaner and Ball (1994). Birds in sleeping posture show a large variation in their degree of alertness, and part of this variation can be attributed to time of year. Particularly in mid-winter (November and December), the behavior of birds in sleeping posture is more characteristic of awakening than quiet sleep (Amlaner and Ball 1994). During this period Gadwalls increase their total time spent vigilant both by increasing peeking frequency (i.e., decreasing the duration of inter-peek intervals) and by increasing the mean duration of peeks. Green-winged Teal also exhibit the same seasonal pattern with maximum values of peeking rates at mid-winter and minimum values during February and March (Gauthier-Clerc et al. 1998). Even in natural conditions, despite predation risk, birds may have to adjust their level of wakefulness in response to physiological constraints. For instance, Metcalfe and Furness (1984) found that foraging migratory Ruddy Turnstones (*Arenaria interpres*) reduced vigilance in order to maximize pre-migratory fattening. We hypothesize that the variation in vigilance and sleep are a result of a trade-off between two opposite requirements: to save energy by sleeping and to monitor the environment, particularly in order to escape from duck aggression and predators. Sleep lowers the metabolic rate and thus induces energy savings (Stahel et al. 1984, Berger and Phillips 1995), even by diminishing levels of vigilance while sleeping (Opp and Ball 1985). Moreover, physiological studies revealed a trade-off between sleep and lipid and protein reserves in birds (Deswasmes et al. 1984, Berger and Phillips 1995). As energy stores decline, wakefulness and drowsiness (the highest energetic and highest alert states) decrease, whereas the duration of slow-wave sleep increases (Deswasmes et al. 1984, Deswasmes et al. 1989). For wintering Gadwalls, the beginning and the end of the winter period are the periods of higher energy demand (Allouche 1988, Tamisier et al. 1995). At the beginning of the winter period, ducks feed intensively and have to recover from severe energy expenses associated with molt and migration and have the lowest weights of the winter (Tamisier et al. 1995). The restoring period lasts two months (September–October) after birds reach their winter quarters (Tamisier et al. 1995). From January to March, despite long daily feeding times and important energy requirements in relation to imminent return-migration and reproduction, their body mass declines because food availability decreases and temperatures are colder (Fox et al. 1992, Tamisier et al. 1995). During these two periods, saving energy by sleeping is given higher priority at the expense of vigilance. This remains consistent with our results showing an increase in the proportion of time invested in sleep compared to vigilance.

In contrast, in mid-winter (November to the beginning of January), when Gadwalls in sleeping posture show a vigilance behavior closer to awakening, they have lower energy demands, showing the highest body mass (more than 30% compared to the beginning of winter) and having the shortest feeding times (Tamisier et al. 1995). Moreover, they perform courtship and pair formation (Paulus 1983, Tamisier et al. 1995) and in the studied marsh also face the highest level of predator disturbance from Marsh Harrier

(*Circus aeruginosus*) and Yellow-legged Gull (*Larus cachinnans*) (Tamisier 1970). As a consequence, an increased vigilance of Gadwalls during mid-winter may also be adapted to monitoring both predators and sexual partners. These predators induced on average 53 take-offs of ducks per day in November 1992 versus 43 in September 1992 in the studied area (Gauthier-Clerc 1998). However, in the mid-winter, an increase in predation disturbance would result in a higher peeking frequency, but not necessarily an increase in the duration of each peek (Hart and Lendrem 1984, Desportes et al. 1993). Moreover, we observed the same seasonal variation in vigilant sleep in Green-winged Teal in another marsh despite no change in predation disturbance. Scanning behavior is an important feature in relation to the detection of predators, but also in monitoring the activities of other members of the group, i.e., in sexual or dominance relationships (Dimond and Lazarus 1974, Elgar 1989). Waking up in sleeping ducks is more often caused by conspecifics (69% of occurrence) than by predators (16%) (Gauthier-Clerc 1998), showing the importance of eye-opening to avoid aggressive interactions with others ducks. Although we have no indication of an increase in aggression during this period in Gadwalls, this interaction is likely to be more frequent during courtship and pairing, that is in mid-winter. However, as most Gadwall are paired in January, we would expect this high level of vigilance to be maintained by males to guard their partner during the end of the winter.

These different factors (body reserves, predator, mating) probably combine to determine the overall seasonal changes in the sleep-vigilance pattern; we can not determine in this study their relative importance. However, our results show that the overall pattern of variation of vigilant sleep of wintering Gadwalls is consistent with energy demand and ecological constraints during the winter. The present study thus confirms that the study of sleep function can benefit from the investigation of the sleep patterns of free-ranging animals (Shaffery et al. 1985). Because such animals are constrained by the demands of survival and reproduction, their sleep patterns may reflect behavioral adjustments to ecological circumstances. The precise relationship between sleep, vigilance, and energy reserves remains to be studied at the individual level and also in nonmigrating duck species. Our results also suggest that the quantification of time-activity budgets in nonbreeding Anatidae (Paulus 1988) may benefit from a more detailed description of sleep patterns.

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