RELATION BETWEEN MIGRATORY ACTIVITY AND ENERGETIC CONDITION AMONG THRUSHES (TURDINAE) FOLLOWING PASSAGE ACROSS THE GULF OF MEXICO[1]

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Abstract. Whereas endogenous time programs are thought to control different aspects of bird migration, regulation of migratory behavior is sensitive to acute ecological factors. The relation between migratory activity and energetic status was studied by monitoring day (presumptive feeding) and night (migratory) locomotor activity of captive North American thrushes (*Hylocichla mustelina, Catharus fuscescens, C. ustulatus,* and *C. minimus*) immediately after spring passage across the Gulf of Mexico. (1) Lean migrants, regardless of species, displayed less night activity than migrants with undepleted fat stores. (2) Lean birds were more active during the day (presumptive feeding behavior) than fat birds, regardless of species. (3) Nocturnal restlessness resumed as lean individuals replenished fat stores, whereas day activity decreased as lean birds regained mass. (4) *Catharus* thrushes, which travel longer distances than Wood Thrushes before reaching breeding grounds, displayed more activity on a per-night basis. Our results support the idea that a migrant's energetic status modifies the programmed course of migration.

Key words: Catharus *thrushes;* Hylocichla mustelina; *migratory activity; energetic condition; stopover biology.*

INTRODUCTION

Migratory birds deposit subcutaneous fat stores that are mobilized as the principal fuel for migratory flight (Blem 1980). Concomitant with the deposition of fat stores, migrants develop migratory activity, which manifests itself as increased locomotor activity or restlessness under captive conditions (see reviews by Berthold 1975, 1990). Endogenous control mechanisms are thought to regulate the circannual pattern of body mass change, including fat deposition, onset and cessation of migratory activity (e.g., Gwinner 1977, 1986, 1990; Gwinner and Czeschlik 1978; Berthold 1984, 1991; Berthold and Querner 1981, 1982), seasonally appropriate migratory orientation (Gwinner and Wiltschko 1978, 1980; Helbig 1992) and may influence seasonal changes in dietary and habitat preferences (e.g., Berthold 1976, Bairlein 1983). Nevertheless, regulation of migratory behavior is sensitive to acute ecological factors (Terrill 1986, Ketterson and Nolan 1985, Sniegowski et al. 1988, Wingfield et al. 1990), including periods of intense energy demand (e.g., Terrill 1987).

We studied the relation between migratory ac-

tivity and energetic status by monitoring day (presumptive feeding) and night (migratory) activity of captive Wood Thrushes (*Hylocichla mustelina*), Veerys (*Catharus fuscescens*), Swainson's Thrushes (*C. ustulatus*) and Gray-cheeked Thrushes (*C. minimus*) immediately after spring passage across the Gulf of Mexico. Nocturnal restlessness in caged landbird migrants corresponds to the daily and annual pattern of natural migratory activity (Berthold 1990, Gwinner 1990), which provides an opportunity for controlled experimentation. When landbird migrants arrive at the northern coast of the Gulf of Mexico in spring, they have just completed a nonstop, 18–24 hr flight of at least 1,000 km (e.g., Buskirk 1980). Many individuals have mobilized most or all lipid stores en route, whereas others have retained fat stores sufficient to continue migration and usually depart the day or night of their arrival (e.g., Moore and Kerlinger 1987, Kuenzi et al. 1991).

Four expectations form the basis of our study: (1) If a bird's energetic status influences the expression of migratory activity, lean (essentially fat-free) migrants should display less migratory activity following trans-Gulf passage than migrants with undepleted stores, regardless of species. If trans-Gulf migrants interrupt migration where the food supply is sufficient to deposit fat

stores, the combination of low fat stores coupled with a high probability of rebuilding stores suppresses migratory activity and induces lean migrants to stay at a stopover site (Biebach 1985; Gwinner et al. 1985; Terrill 1986, 1990).

(2) To the extent that daytime activity of caged migrants reflects feeding behavior, lean birds should be more active during the day than fat birds, regardless of species. This expectation is based on the premise that birds in migratory disposition should adjust their feeding behavior to meet the energetic requirements of migration (e.g., Moore and Simm 1985, 1986; Loria and Moore 1990; see King and Murphy 1985). Just as hyperphagia mediates pre-migratory fat deposition (King and Farner 1963), birds that have mobilized essentially all of their fat stores while crossing the Gulf of Mexico should increase their rate of feeding.

(3) If migratory activity is related to sufficient energy stores (Berthold 1986), we expect lean birds to resume migratory activity as soon as they regain mass (restore fat deposits) under conditions of ad libitum food. Biebach (1985) has hypothesized that migratory activity resumes only after fat levels exceed some "setpoint" or threshold, which may vary over the course of migration (sensu Mrsovsky and Powley 1977). We also expect a concomitant decrease in daytime (presumptive feeding) activity among lean birds because of decreased motivation to feed in relation to other activities, e.g., resting, predator avoidance and resumption of migration (cf. McCleery 1977, Sibley and McFarland 1976).

(4) Different species produce different amounts of migratory activity in ages, and long-distance migrants produce more activity than short distance migrants (Gwinner 1986; Berthold 1973, 1986). Catharus thrushes migrate longer distances and must travel, on average, further beyond the Gulf of Mexico before reaching their breeding grounds than Wood Thrushes. If the amount of migratory activity is positively correlated with migratory distance, Catharus thrushes should display more nights of activity. Alternatively, Catharus thrushes might display more activity each night than Wood Thrushes. It is this latter expectation that we examined.

METHODS

Mist-nets (12 × 2.6 m, 30 mm mesh) were used to capture thrushes after the spring trans-Gulf migration in 1990 in a coastal woodland (Peveto

Woods) located in Cameron Parish, Louisiana (29°45′N, 93°37′W). After capture, 34 Wood Thrushes, 7 Veerys, 12 Swainson's Thrushes, and 11 Gray-cheeked Thrushes were placed individually in cages (30 × 38 × 38 cm) and housed in an outdoor aviary located 1 km from Peveto Woods. Birds were fed ad libitum with a mixed diet of meal worms (Tenebrio molitor), sow bugs (Armadillidium vulgare), dewberry (Rubus trivialis), and moistened monkey biscuits (Hill's Products). Water was available at all times. Individuals were released at Peveto Woods within 7 days of their initial capture.

Each cage was equipped with two horizontal perches centered in the cage and oriented at right angles to one another. The perches were attached to microswitches, which allowed us to monitor locomotor activity over the 24-hr day using an event recorder. Activity was recorded over 3 days and nights. The diel pattern of activity was divided into daytime (06:00–20:00 CST) and nighttime (20:00–06:00 CST). Catharus thrushes were grouped for analysis because of small samples and similar migratory distances relative to the Wood Thrush. The inclusion of Wood Thrushes and Catharus thrushes in our study provides constructive replication, which strengthens inferences drawn from the results.

Individuals were assigned to "lean" or "fat" groups depending on whether or not visible subcutaneous fat was depleted (Table 1). We quantified fat according to a six-point scale developed by Helms and Drury (1960). Such scoring provides a reliable method of indexing fat as long as comparisons are made within species and variability among observers is controlled (Krementz and Pendleton 1990). Body mass was determined to the nearest 0.1 g using an electronic balance.

An iterative, weighted least-squares regression procedure, based on size-corrected (body mass ÷ wing chord³) mass of fat-depleted thrushes, was used to estimate fat-free body mass of free-ranging individuals (Yong 1993) in order to determine flight ranges (sensu Pennycuick 1989). We calculated an individual's fat load by subtracting estimated fat-free mass from the body mass measured upon capture.

Lean Wood Thrushes averaged 38.80 g, which is close to the fat-free body mass (38.06 g) previously reported for the species (Child 1969), whereas fat individuals averaged 7 g above fat-free mass (Table 1). Assuming the difference be-

TABLE 1.   Body mass (mean ± 1 SE) (n) at time of initial capture, estimated migratory distance, average gain in mass during the three-day experiment, and average (mean ± 1 SE) daytime and night activity of lean (fat score = 0) and fat (fat score ≥ 2) Wood Thrushes and Catharus thrushes.

	Wood Thrush		Catharus Thrushes	
	Lean (18)	Fat (17)	Lean (17)	Fat (13)
Fat-free mass[a] (g)	38.06		23.66	
Mass (g)	38.80 ± 1.03	45.19 ± 0.87	25.01 ± 0.79	29.66 ± 0.48
	t = 4.71**[b]		t = 4.66**	
Flight range (km)[c]	100	820	276	1,120
Mass gain (g)[d]	3.16 ± 0.61	0.01 ± 0.52	3.45 ± 0.83	-0.33 ± 0.39
	t = 3.91**		t = 3.74**	
Night activity[e]	4.33 ± 1.08	12.37 ± 1.77	8.5 ± 1.38	16.76 ± 1.27
	t = 5.30**		t = 4.27**	
Day activity[e]	16.11 ± 1.19	10.89 ± 1.56	12.36 ± 0.85	8.28 ± 0.59
	t = 3.95**		t = 3.87**	

[a] See Child (1969) and Hicks (1967).
[b] ** $P < 0.01$.
[c] See Pennycuick (1975).
[d] Body mass upon release minus body mass upon initial capture.
[e] Mean number of 2 min periods with activity per hour.

tween the estimated fat-free mass and the average body mass for lean and fat birds represents fat available for migratory flight, an average fat individual has an estimated flight range 850 km greater than an average lean individual (sensu Pennycuick 1975). Fat Catharus thrushes were, on average, 4.6 g heavier than lean Catharus thrushes, which translates into an 810 km difference in estimated flight range (Table 1).

RESULTS

WITHIN-GENUS ANALYSIS

Fat birds did not gain mass while in captivity, regardless of species, whereas lean birds gained, on average, more than 3 g during the three-day experiment. This corresponded to 8% and 13% of lean body mass for Wood Thrush and Catharus thrushes, respectively. Lean birds displayed significantly less activity at night than fat birds each night of the experiment (Figs. 1, 2; Table 1). Fat birds were active throughout each night, with the possible exception of the second for Wood Thrush, when activity declined the second half of the night. Night activity of lean birds increased during the experimental period, and was most pronounced during the first half of the night for both Wood Thrushes and Catharus thrushes (Fig. 2). The increase in night activity among lean birds over test days was significant for both Wood Thrushes ($F = 7.77$, df = 2, 51, $P < 0.01$) and Catharus thrushes ($F = 6.32$, df = 2, 48, $P < 0.01$). Planned comparisons revealed significant differences in night activity be-

tween test-days two and three for lean Wood Thrushes ($t = 3.36$, df = 51, $P < 0.05$) and lean Catharus thrushes ($t = 2.01$, df = 48, $P < 0.05$), but not between the first and second test-days (i.e., test-day 1 = test-day 2 = test-day 3).

During the day, lean birds were more active than fat birds on all test days (Table 1; Fig. 3), but the third test day for Catharus thrushes. The difference between fat and lean birds in daytime activity diminished by the end of the experiment, especially among Catharus thrushes.

BETWEEN-GENERA ANALYSIS

Catharus thrushes displayed more nocturnal activity than Wood Thrushes ($t = 2.20$, df = 63, $P < 0.05$) (Fig. 2), regardless of energetic status. When night activity is examined in relation to estimated fat load, fatter birds were more active, especially among Catharus thrushes (Fig. 4A). Individual variation in activity among Catharus thrushes also increased in relation to larger fat stores.

Average fat load relative to lean body mass is significantly higher among Catharus thrushes (23%) than Wood Thrushes (15%) upon release (i.e., after replenishing energy stores): $t = 2.57$, df = 63, $P < 0.05$. An estimate of flight distance depends on the migrant's fat load and wing morphology (see Pennycuick 1989). To the extent that cage activity reflects migratory activity, the amount of night activity should be positively correlated with migratory range. Catharus thrushes able to fly further were more active, but that
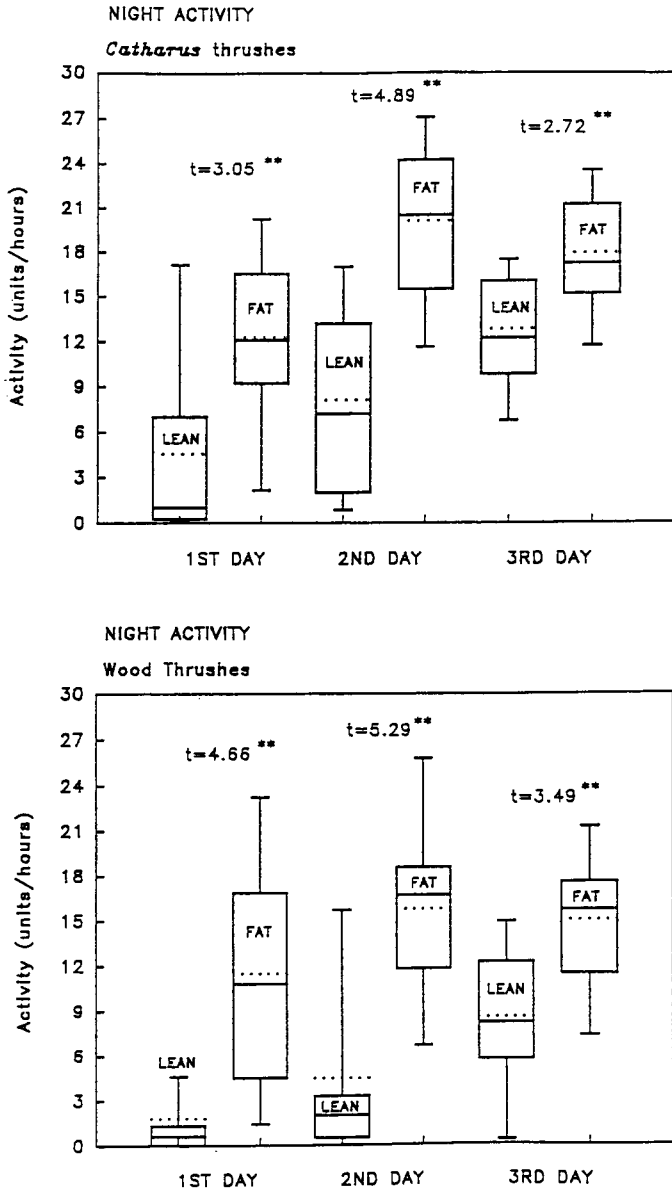
FIGURE 1.   Night (migratory) activity of fat ($n = 17$ Wood Thrushes, 13 *Catharus* thrushes) and lean ($n = 18$ Wood Thrushes, 17 *Catharus* thrushes) birds. Median (dashed line), mean (solid line) ± 1 SE and 95% confidence interval given. Activity expressed as number of 2 min periods during which activity occurred per hour.

relationship is not evident among Wood Thrushes (Fig. 4B).

DISCUSSION

ACTIVITY AND ENERGETIC CONDITION

Energetic status affected the nighttime (migratory) and daytime (foraging) activity shown by Wood Thrushes and *Catharus* thrushes after passage over the Gulf of Mexico. Lean birds were less active at night than were fat birds, although the disparity between groups decreased as lean birds rebuilt depleted stores (i.e., regained body mass). Conversely, lean birds were more active than fat birds during daylight hours. The observed differences in daytime and nighttime ac-

WOOD THRUSH: 1ST NIGHT

ACTIVITY (UNITS/HR)

CATHARUS THRUSH: 1ST NIGHT

ACTIVITY (UNITS/HR)

WOOD THRUSH: 2ND NIGHT

ACTIVITY (UNITS/HR)

CATHARUS THRUSH: 2ND NIGHT

ACTIVITY (UNITS/HR)

WOOD THRUSH: 3RD NIGHT

ACTIVITY (UNITS/HR)
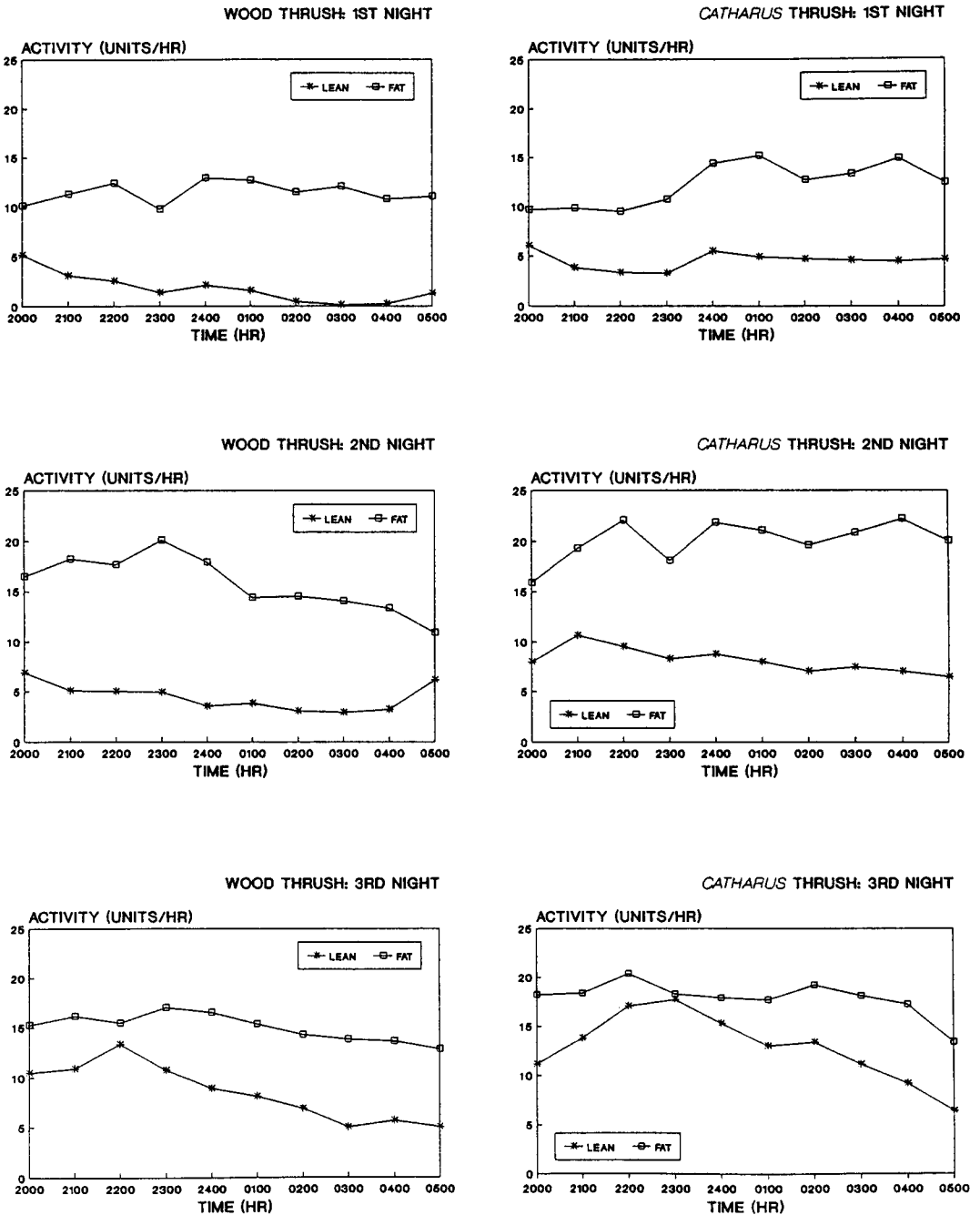
CATHARUS THRUSH: 3RD NIGHT

ACTIVITY (UNITS/HR)

FIGURE 2. Hour-by-hour pattern of night activity for fat and lean thrushes. Activity expressed as number of 2 min periods during which activity occurred per hour.

tivity between fat and lean thrushes are consistent with evidence that lean birds interrupt their migration to replenish energy stores depleted during flight.

Several field studies have reported that migrating birds are more likely to stopover beyond the day of initial capture when fat stores are low (e.g., Cherry 1982, Pettersson and Hasselquist
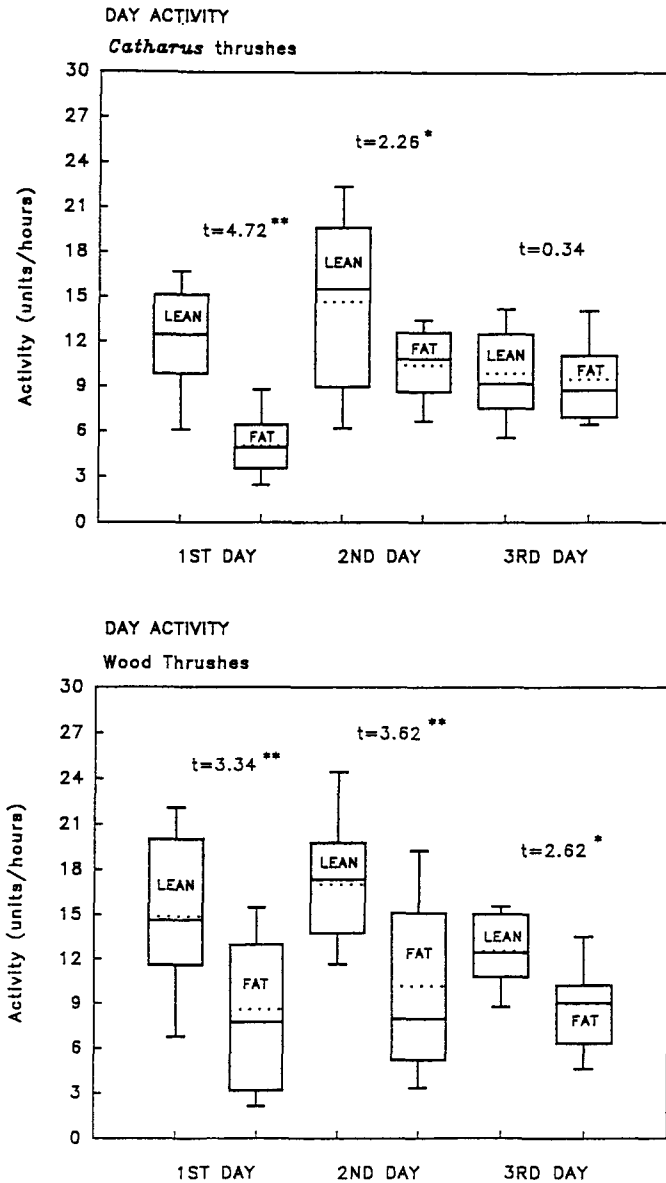
DAY ACTIVITY

Catharus thrushes

DAY ACTIVITY

Wood Thrushes

FIGURE 3. Day activity of fat ($n = 17$ Wood Thrushes, 13 *Catharus* thrushes) and lean ($n = 18$ Wood Thrushes, 17 *Catharus* thrushes) birds. Median (dashed line), mean (solid line) ± 1 SE and 95% confidence interval given. Activity expressed as number of 2 min periods during which activity occurred per hour.

1985, Bairlein 1985, Biebach 1985, Biebach et al. 1986, Moore and Kerlinger 1987, Kuenzi et al. 1991). Presumably birds with sufficient fat stores rest during daylight hours and continue migrating the night following arrival (sensu Alerstam and Lindström 1990), whereas birds with little or no fat actively feed to regain some fat before showing migratory activity.

Length of stopover also depends on habitat suitability and the likelihood of regaining lost mass (Moore and Simons 1992). Lean migrants may be better off continuing their migration when they are unable to find sufficient food or when competition precludes access to sufficient food (see Rappole and Warner 1976, Terrill 1986, Moore and Yong 1991). Food deprivation stud-
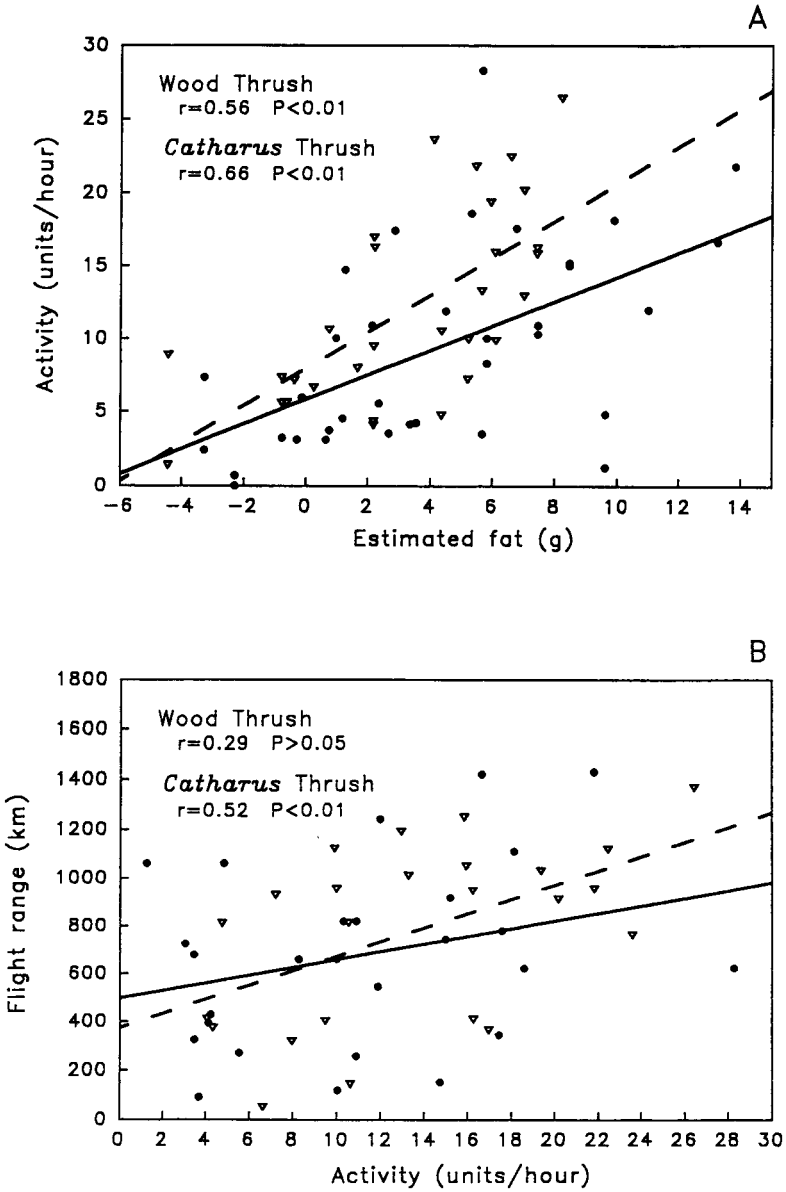
FIGURE 4. Regression of night activity against estimated available fat (A) and flight range against night activity (B) for Wood Thrushes (solid symbols, solid line, $n = 35$) and *Catharus* thrushes (open symbols, dashed line, $n = 30$). Estimated fat determined by subtracting estimated fat-free mass from body mass at initial capture. Negative fat values indicate that body mass was below fat-free mass for some individuals when first captured. Flight ranges were calculated according to Pennycuick (1989) and depended on wing span, estimated fat load, and estimated fat-free mass of each individual.

ies with captive migrants confirm a relationship between energetic condition and migratory activity that is dependent on the presence of food (e.g., Biebach 1985) or factors which affect access to food (e.g., Terrill 1987).

Whereas it is not surprising that a bird's energetic state affects the likelihood of undertaking a night's migration, the relationship is not a simple one. Migratory activity and deposition of fat may develop through separate regulatory sys-

tems of circannual rhythmic control (King and Farner 1963, Berthold 1975). Modifying energetic condition may have no direct effect on the activity patterns because the two are under separate endogenous control. Preventing fat accumulation may diminish the intensity of activity but may not eliminate it completely (e.g., King and Farner 1963).

In addition, the relation between migratory activity and energetic status is influenced by the migrant's situation vis-a-vis geographical barriers (Alerstam 1990). For example, lean Indigo Buntings (*Passerina cyanea*) captured in fall prior to passage across the Gulf of Mexico produced little or no nocturnal activity (Moore and Kerlinger 1990). When they did, they oriented north as often as south. Lean Indigo Buntings that had crossed the Gulf of Mexico in spring were nocturnally active in a seasonally appropriate northward direction, although the amount of activity was not quantified. The behavior of Indigo Buntings is similar to that of European Robins (*Erithacus rubecula*) in relation to the Baltic Sea in autumn (Sandberg et al. 1988, Karlsson et al. 1988). Birds that had arrived on the southern coast of Sweden by overland migration were lean and headed north during orientation cage tests rather than in a seasonally appropriate southerly direction, which would take them across the Baltic Sea. This behavior was interpreted as re-orientation of lean migrants in response to an ecological barrier (Sandberg et al. 1988; see also Alerstam 1978, Lindström and Alerstam 1986). Robins that interrupted their flight over the Baltic Sea to stop at Ottenby along the east coast of Sweden were heavier than Falsterbo birds and oriented their activity in a seasonally appropriate southwesterly direction.

Finally, Able (1977) found no correlation between the amount of nocturnal activity and fat load while conducting cage orientation experiments with grounded landbird migrants on Block Island (USA) along the Atlantic coast in autumn. He did report a significant relationship between fat load and the likelihood an individual would display oriented activity.

Whereas our experiment was not specifically designed to determine whether a "setpoint" mechanism (sensu Biebach 1985) controlled resumption of activity among migrating thrushes (i.e., we measured mass only upon capture and after the experiment and quantified activity for only three nights), certain findings are relevant.

(1) The statistical outcome of planned comparisons across days is not inconsistent with such a mechanism (i.e., lean birds resumed migratory activity on third night, two days after food and the opportunity to replenish fat stores existed). (2) Yet, lean birds were not as active as fat birds when they did resume migratory activity on the third night of captivity. Regardless of species, the activity of "lean" birds approximated levels of fat birds only during the first half of the night, and declined later in the night. (3) When we examined night activity in relation to estimated fat load for Wood Thrushes and *Catharus* thrushes, activity was directly related to the amount of available energy (fat). The distribution of data does not suggest a step function indicative of a threshold or "setpoint." Although resumption of migratory activity may depend on a "setpoint" sensitive to the amount of stored energy, the intensity of activity appears to vary in relation to amount of fat present.

Certain factors might obscure recognition of a "setpoint" under conditions of our study: (1) The "setpoint" for nocturnal activity may be relatively low and variable after passage across the Gulf of Mexico and (2) variation may exist among individuals. However, because of body mass variation among individuals within a given species, the "setpoint" for different individuals may result in a continuous distribution when individuals are pooled.

ACTIVITY AND MIGRATORY DISTANCE

Clear differences in migratory range between Wood Thrushes and *Catharus* thrushes led us to expect corresponding differences in the amount of night activity. *Catharus* thrushes displayed more activity per night than Wood Thrushes, regardless of energetic status, a result consistent with published work on other species (see Berthold 1990, Gwinner 1990). For example, populations of Blackcaps (*Sylvia atricapilla*) originating from different breeding grounds showed positive correlation not only between migratory distance and total nocturnal activity per season, but also between migratory distance and daily nocturnal activity (Berthold and Querner 1982).

The observed difference between *Catharus* thrushes and Wood Thrushes may also reflect a relationship between night activity and available fat: *Catharus* thrushes averaged larger fat loads relative to lean body mass than Wood Thrushes. If the amount of night activity reflects distance

migrated, then a close correlation should exist between activity and estimated range based on aerodynamic principles and estimated fat load. We found this to be true for *Catharus* thrushes as a group. Individuals which could be expected to migrate greater distance based on their fat load also showed more activity.

We also suspect that the relationship between migratory activity on a night-to-night basis and migratory range may break down as individuals near the end of their migration. Variation in fat load among Wood Thrushes, for example, may be related to factors other than migratory distance, including the exigencies of trans-Gulf passage. Some birds arrive with stores in excess of what was necessary to complete the journey (Moore and Kerlinger 1990) and extra fat stores may provide a margin of safety related to events on the breeding grounds.

ACKNOWLEDGMENTS

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