

MASS VARIATION IN BREEDING WOOD THRUSHES¹

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Abstract. Data from a 15-year study of breeding Wood Thrushes (*Hylocichla mustelina*) indicate that body mass varies with sex, year, time of day, and breeding stage. The pattern of mass variation with breeding stage differs for the two sexes. Mean female mass is low during the prebreeding stage (50.3 g), but increases rapidly, reaching its highest level in the laying stage (57.4 g). It is reduced during the incubation (54.2 g) and feeding stages (51.1 g), rises again in the break between broods (53.6 g), but declines in the postbreeding period (50.7 g). Male mass is lowest in the prebreeding stage (46.5 g), but slightly higher in the laying period (48.0 g). It increases in the incubation period (49.4 g), then declines in the feeding (48.3 g) and break stages (47.2 g), but reaches its greatest level in the postbreeding period (49.9 g). Both sexes may be physiologically stressed during the feeding stage, but male stress is probably greater in the prebreeding and break stages.

Key words: Wood Thrush; *Hylocichla mustelina*; mass; mass variation; breeding; reproductive effort; reproductive costs.

INTRODUCTION

Ornithologists have studied mass variation in wild birds for over half a century: Baldwin and Kendeigh (1938) give an early review. Among factors known to affect bird mass are sex, age, habitat, year, season, time of day, and breeding, molting, and migratory activities (Clark 1979). Recently, patterns of mass change during the breeding season have been studied in relation to reproductive effort.

A fundamental principle of life history theory is that current reproductive effort has costs that decrease future reproduction (Stearns 1976). These costs may be a loss of physiological condition or an enhanced risk of predation. An assumption of many studies of altricial birds is that these costs occur mainly during the period when young are fed. Many studies have shown that parent birds lose mass while feeding young, and this mass loss has often been interpreted as indicating physiological stress (see Ricklefs 1974). Experiments manipulating brood size often confirm that parents feeding more young lose more mass than those feeding fewer young (e.g., Hus-sell 1972, Askenmo 1977, Schifferli 1978, Bryant 1979, Westerterp et al. 1982, Nur 1984). A few studies have demonstrated decreased parental survival (Askenmo 1979, Nur 1984) or subsequent reproduction (Slagsvold 1984) with in-

creased brood size. Other authors, however, have failed to find greater parental mass loss (DeSteven 1980, Freed 1981), reduced energy reserves (Ricklefs and Hussell 1984), or lower survivorship (DeSteven 1980, Smith 1981) with increased brood size.

A few authors have suggested that other parts of the breeding cycle may also cause stress or enhance predation risk (Jones and Ward 1976, Martin 1987). Territorial, courtship, mate-guarding, egg-laying, and incubation behaviors all require changes in energy and activity budgets that may engender reproductive costs. In this paper we examine sex, breeding stage, age, year, and time of day as sources of mass variation in adult Wood Thrushes (*Hylocichla mustelina*), using 15 years of data from a site in northern Delaware. Patterns observed suggest that the period when young are fed may create a negative energy balance for both sexes in Wood Thrushes, but that other stages may be more stressful for males.

STUDY SITE AND METHODS

Our studies were made at the University of Delaware Woodlot (UDW) located on the University Farm in Newark, Delaware. This 16-ha area was agriculturally abandoned about 1900 (Steinhauer 1974). Predominant vegetation and bordering conditions changed little during the study. *Liriodendron tulipifera*, *Liquidamber styraciflua*, *Acer rubrum*, *Quercus alba*, and *Quercus rubrum* dominate the tree canopy, though die-off of the latter two became conspicuous about 1985. *Cor-*

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² Order of authorship was determined by a coin toss.

TABLE 1. Definitions of breeding stages used in this study. The activities listed are the principal nonmaintenance behaviors during each stage. Those without a literature reference are based on our own observations.

Stage	Definition	Male activities	Female activities
Prebreeding	Arrival—day before first egg laid.	Territory defense, ^{b,c} courtship, ^{a,b} follows female, ^{b,c} sings often. ^f	Courtship, ^b nest building. ^{a,c}
Laying	Day first egg laid—day last egg laid.	Follows female, ^b copulates, ^b sings often. ^f	Forming and laying eggs.
Incubation	Day after last egg laid—day before first egg hatched.	Sentry duty, ^{a,c} guards nest, ^{a,c,d} some singing. ^f	Incubates 60–90% of day, ^{a,c,d} may defend nest. ^a
Feeding	Day first egg hatched to 6th day after young fledged.	Does 60–75% of feeding, ^{a,d,e} defends young, ^{b,c} limited singing. ^f	Broods young, ^{a,b} 25–40% of feeding. ^{a,d,e}
Break	Day nest lost or 7th day after first young fledged—day before first egg of next clutch laid.	Frequent singing, pair-maintenance behavior, accompanies female, possible territory adjustment.	Nest building.
Postbreeding	Days following nest loss or 7th day after fledging from last nest.	Some are molting.	Some are molting.
Unknown	Probably breeding on site but not assignable to a nesting stage with available information.		
May transients	Caught one or two times within a few days in May and not observed again.	Presumed to be migrating, not breeding at UDW.	Presumed to be migrating, not breeding at UDW.
Late transients	Caught one or two times within a few days after May and not observed again.	Presumed not to be breeding at UDW.	Presumed not to be breeding at UDW.

^a Brackbill 1943.^b Weaver 1949.^c Brackbill 1958.^d Nolan 1974.^e Knopf 1974.^f Watson 1987.

nus florida and *Carpinus caroliniana* are important in the subcanopy. *Viburnum* spp., *Clethra alnifolia*, *Lindera benzoin*, and *Smilax* spp. compose most of the shrub layer. Agricultural and athletic fields surround 95% of the site. A highway along the remaining edge, and a residential development beyond, separate UDW from the nearest habitat occupied by Wood Thrushes, 0.6 km away. For more details see Longcore et al. (1966) and Gorman and Roth (1989).

Our data came from a long-term study of Wood Thrush breeding ecology that included a yearly effort to ensure all Wood Thrushes breeding in UDW were color-banded and their territories and nests identified. Fieldwork was conducted from 1974–1988. It began each spring when Wood Thrushes returned to UDW in late April and ended after the last nest was finished in August. Our earliest capture of a Wood Thrush was 28

April and the latest 26 August (though only five captures occurred after 11 August). Each year we tried to locate, determine the ownership of, and monitor all Wood Thrush nests in UDW. We are confident that few nests escaped our discovery, except in 1979 (see below). For each nest we determined the dates of egg laying, hatching, fledging, or failure.

When birds were mist-netted, we weighed them to the nearest 0.1 g on a triple-beam (1974–1979) or nearest 0.5 g on a Pesola spring balance (1980–1988), examined them for brood patch or cloacal protuberance to determine sex, and recorded the date and time of the capture. We post facto assigned a breeding stage to each capture based on our records of the bird's breeding activities on the date of the capture. We recognized nine activity stages; these are defined in Table 1.

The data set had the following limitations. Lit-

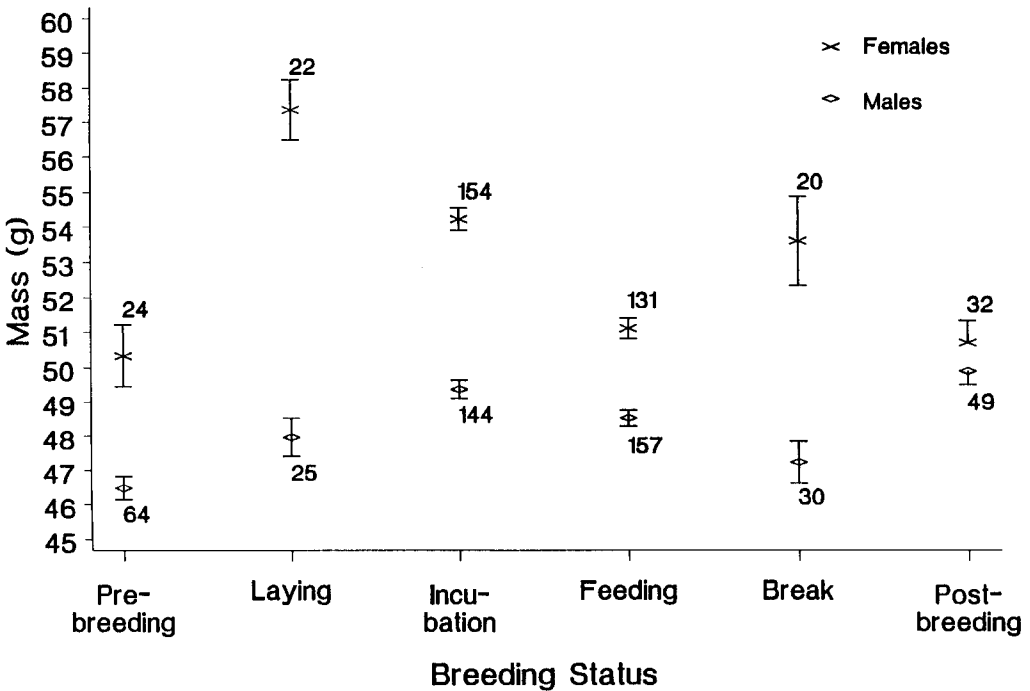


FIGURE 1. Mass variation of Wood Thrushes by breeding status. Breeding statuses are defined in Table 1. Crosses and diamonds designate means, vertical bars represent \pm one standard error, sample sizes are given above (females) or below (males) the error bars.

tle effort was made to find nests in 1979, though we actively netted to maintain a banded adult population. Thus most captures from 1979 fell into the "unknown" breeding stage. In 1980-1983 we did not net or seek nests in a 3-ha peninsular portion of UDW that typically had held two or three pairs of Wood Thrushes. The mass data collected 1 May-11 June 1983 were lost in a theft, so we have fewer records from that year.

Our analyses omit records in the unknown and both transient categories, except as otherwise indicated. Of the many birds recaptured over the course of the study, we excluded from these analyses only the few cases in which a bird was captured a second time in one day. The remaining data include 852 captures of 263 Wood Thrushes. Analyses of variance and covariance were performed using Type III sums of squares of the SAS General Linear Models procedure (SAS 1982). These estimate the significance of each factor while adjusting for all other factors.

RESULTS

Females were heavier than males overall (female \bar{x} = 52.8 g, SE = 0.22; male \bar{x} = 48.5 g, SE = 0.15) and variation with breeding stage differed

in pattern between the sexes (Fig. 1). The differences in mass between the sexes, among stages, and in the interaction between the two were all highly significant (two-way ANOVA, P 's < 0.0001). Females were heavier than males at every breeding stage (t -test, P 's < 0.0001) except postbreeding (t -test, P > 0.25). Given these differences, we will analyze the sexes separately for the remainder of the paper.

Females weighed significantly more when laying than at any other time. They also weighed more during incubation and break periods than during prebreeding, feeding, or postbreeding periods (t -test, P 's < 0.05). In the three latter stages the females had notably similar masses (Fig. 1). The pattern for males can be summarized by ranking the stages by mean mass (postbreeding > incubation > feeding > laying > break > prebreeding) and noting that mass for each stage is significantly different from all those not adjacent to it in rank (t -test, P 's < 0.05).

Our sampling of Wood Thrush masses was not systematic with respect to breeding stage, age, year, or time of day, making it important to consider whether the observed breeding stage patterns could have been affected by other factors.

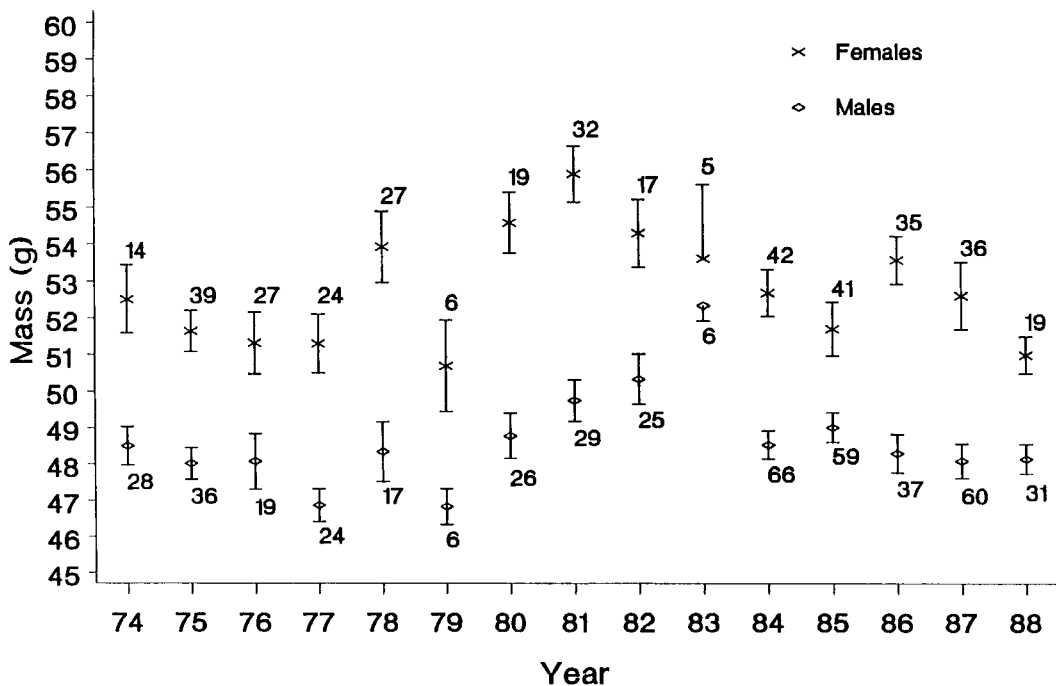


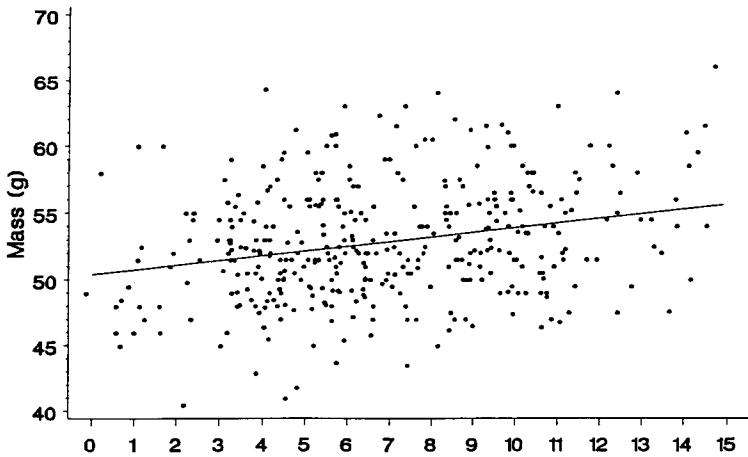
FIGURE 2. Mass variation of Wood Thrushes by year. Crosses and diamonds designate means, vertical bars represent \pm one standard error, sample sizes are given above (females) or below (males) the error bars.

To evaluate age we classified the birds as first-time breeders, i.e., birds breeding for the first time at UDW, and senior breeders, i.e., birds that had bred at UDW in one or more previous years. For this analysis we omitted data from 1974 and 1984; birds first captured in 1974, the first year of the study, could have bred on the site in previous years without our knowing it, and our failure to study the peninsular portion from 1980–1983 made it similarly difficult to assign age classes when we resumed studying this area in 1984. Among the remaining birds we found no significant differences between first-time and senior breeders and no significant interaction between age and breeding stage for either sex (two-way ANOVAs, P 's > 0.05). As age does not contribute significantly to mass variation, we will not consider it further.

A second factor that might have contributed to the observed patterns was annual variation. Significant differences in mass existed among years for both sexes (one-way ANOVAs, P 's < 0.0001). Notable deviations were two below average years, 1977 and 1979, and several above average years, especially 1980–1983 (Fig. 2). We did not have sufficient data to test for interactions

between breeding stage and year within each sex. Such interactions, if they occurred, probably did not strongly affect the differences we observed between mean masses at different breeding stages. Annual variation might have arisen from occasional bouts of size-selective mortality during nonbreeding periods (Boag and Grant 1981, Johnston and Fleischer 1981), but such effects should have been equal for all breeding stages. Feeding conditions on the breeding grounds might have caused birds to be fatter at some times than others, and such variations within a year might have contributed to differences between breeding stages. However, the laying, incubation, feeding, and break stages all overlap from the last week of May through the second week of July, so that variations in feeding conditions during this period would have affected birds in all these stages. Favorable (or unfavorable) conditions early in a season would have had a disproportionate effect on prebreeders (and, to a lesser extent, on laying birds), as would such conditions late in the season on postbreeders. By averaging over 15 years, however, the influence of any good seasons on our data is likely to have been counterbalanced by the effect of poor seasons.

a. Females



b. Males

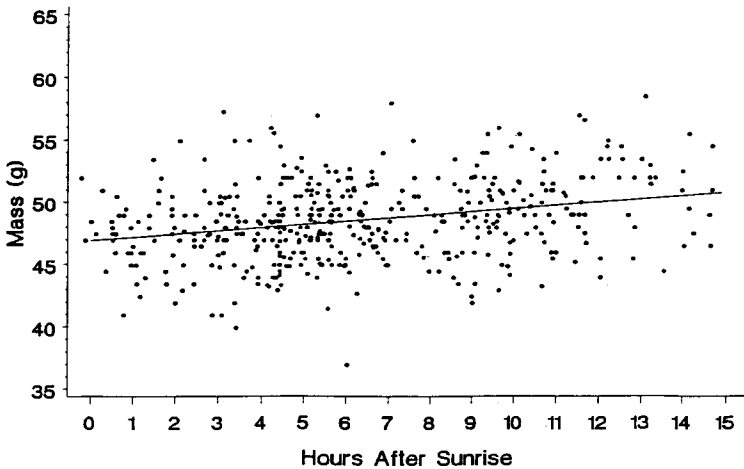


FIGURE 3. Mass variation of Wood Thrushes by time of day. Data are over all breeding stages. Correlation and regression statistics are given in Table 2.

We standardized the time of capture as hours after sunrise to test for the effect of time of day on mass. For both sexes mass was positively correlated with time of capture when data from all breeding stages were combined (Fig. 3), though the r^2 s were quite low (Table 2). When the data were broken down by breeding stage, not all of the correlations were significant, and in no case was more than 18% of the variance in mass explained by the time of capture (Table 2). Linear regressions of mass on time of capture have slopes that differ somewhat for the different breeding stages (Table 2), but the lack of a significant interaction between breeding stage and time of cap-

ture (ANCOVA, P 's > 0.8 for both sexes) indicates that differences in the rate of daily mass gain did not contribute substantially to the differences observed between breeding stages.

Year or time of day still could have influenced our results if we happened to capture birds of a particular breeding stage more often during years or times of day when masses were typically low or high; e.g., if we captured prebreeding males early in the day more often than we captured males of other breeding stages early in the day, prebreeding males would have had a lower mean mass for this cause alone. The linear models approach to ANOVA allows us to control for such

TABLE 2. Correlation and linear regression statistics of mass of Wood Thrushes on time of day for each breeding stage.

Stage	<i>n</i> *	<i>r</i> ²	<i>P</i>	Y-intercept	Slope
Females					
Overall	378	0.064	0.0001	50.4	0.348
Prebreeding	22	0.162	0.0633	47.4	0.423
Laying	22	0.002	0.8461	57.9	-0.069
Incubation	152	0.034	0.0297	52.7	0.232
Feeding	130	0.073	0.0019	49.1	0.292
Break	20	0.115	0.1446	50.1	0.500
Postbreeding	32	0.065	0.1603	48.9	0.303
Males					
Overall	465	0.076	0.0001	46.9	0.255
Prebreeding	63	0.047	0.0890	45.5	0.193
Laying	25	0.080	0.1706	46.4	0.235
Incubation	143	0.079	0.0007	47.7	0.267
Feeding	155	0.044	0.0088	47.3	0.187
Break	30	0.175	0.0216	44.4	0.392
Postbreeding	49	0.178	0.0025	48.2	0.288

* Some sample sizes are less than in Figure 1 because the time of capture was not recorded in all cases.

effects, and the analysis indicates that they were slight. Controlling for differences due to the year and time of day of each capture, mean mass at each breeding stage changed very little (we do not present these data as the patterns are almost identical to those in Fig. 1), and breeding stage still contributed highly significantly (three-way ANOVAs, $P < 0.0001$) to variation in mass for both sexes. The only changes from our initial analysis were in the significance of differences between male breeding stages. The order of the mean masses ranked by stage remained unchanged, and postbreeding birds remained significantly heavier than all but incubating birds, which became significantly heavier than all but postbreeding and laying birds (rather than postbreeding and feeding birds). Laying, feeding, and break birds did not differ significantly from each other, but prebreeding birds remained lighter than all but break birds.

The relatively low masses observed in the prebreeding stage might have reflected the capture of birds that had recently completed long migratory flights that depleted their fat reserves. To test that possibility we compared the masses of prebreeding males with those of May transient males. The May transients ($\bar{x} = 48.9$ g, $SE = 0.89$, $n = 23$) weighed significantly more than the prebreeding birds (t -test, $P < 0.05$). Having only three May captures of transient females precluded a similar analysis for them.

DISCUSSION

Lacking data on body composition, we cannot give a precise account of the sources of mass variation in breeding Wood Thrushes. In addition, averaging over many years may conceal important events that only occur in extreme years. Despite these limitations, by making the assumption that fat and gonadal mass changes in Wood Thrushes are generally similar to those observed in other passerines, we can hypothesize that significant physiological stress as manifested by decreased body mass is likely a regular occurrence during some breeding stages but not others.

Male and female Wood Thrushes have masses that do not differ significantly in winter, though males tend to be slightly heavier and their wing chords average slightly longer (Rappole 1988). Within a few days of their arrival at UDW, however, prebreeding females weigh about 4 g more than the males. Both sexes probably have rapidly enlarging gonads at this stage (Wingfield and Farner 1978, Wingfield 1983), and females likely increase their fat reserves (Jones and Ward 1976, Wingfield and Farner 1978). Despite increasing testes mass, males are probably losing weight overall, as suggested by their low mass relative to transient males. Territorial and courtship activities probably cause a negative energy budget and decreasing fat reserves for males at this stage

(Nice 1937, von Haartman 1954, Jones and Ward 1976, Hogstad 1982). Mass of both sexes is greater during the laying period. The increase in the mean mass of the females is due primarily to further growth of the ovaries and oviduct and the weight of developing eggs (Wingfield and Farner 1978, Wingfield 1983, Ricklefs and Hussell 1984). Testes mass reaches its maximum during this stage, and its increase must account for most or all of the increase in male mass. We are unable to estimate whether either sex gains or loses fat in the laying stage. The very active singing and mate guarding in this period, however, would probably be at least demanding enough to keep males' fat reserves near prebreeding levels.

During incubation, ovaries and oviduct partially regress and females no longer carry large ova and follicles; these factors probably account for much of the decrease between the laying and incubation stages (Ricklefs 1974, Ricklefs and Hussell 1984, Wingfield and Farner 1978). Incubation is probably a period of neutral or even positive energy balance (Walsberg 1983). Ovaries and oviduct probably remain somewhat enlarged, however, at least while first broods are incubated and fed (Wingfield and Farner 1978). Thus, although the mass of females feeding young is no less than that of pre- and postbreeding females, feeding-stage females probably have larger reproductive organs and somewhat smaller fat reserves, the fat loss indicating a negative energy balance. Male mass increases during the incubation stage despite the probable regression of the testes (Wingfield and Farner 1978), suggesting that they deposit fat during this period when they are less active. The slightly lower mass during the feeding period may indicate that males return to a negative energy budget.

In the break between broods females probably begin to replenish fat reserves and reproductive organ mass, accounting for the overall greater mass of females at this time. Males again engage in courtship and territorial behavior, leading to mass decline. Postbreeding females probably rebuild fat reserves as their ovaries and oviduct shrink, with little net change from the feeding stage. Males seem to recover fat reserves, reaching their greatest total mass. Some of our postbreeding birds were molting, and this may have raised masses slightly (Payne 1972).

We conclude that both sexes may experience a negative energy balance during the feeding stage.

Mass loss at this stage, however, may have benefits in promoting efficient flight (Freed 1981, Norberg 1981). Males are probably more stressed during the prebreeding and break periods. Our data do not preclude the possibility that Wood Thrushes have other costs of reproduction. Physiological stress during other stages may occur in years of low food supply, or reproduction may increase predation risk during one or more stages. Establishing a robust model of reproductive effort in altricial birds will require much experimental work with a variety of species, but such work is needed on all stages of the breeding cycle, not just the feeding stage.

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