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Nutrient reserves, probability of cold spells and the question of reserve regulation in wintering canvasbacks

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Summary

1. Interpreting body mass and composition of wintering birds is often confounded by the inability to discriminate endogenous regulation of reserves from effects of proximate weather and food conditions. Endogenous regulation is thought to act through genetically controlled set-points that change throughout the year, due to evolutionary adaptation to long-term probabilities of needing reserves at different times.

2. For canvasbacks (*Aythya valisineria*) wintering in upper Chesapeake Bay, coastal North Carolina, and Louisiana, I calculated over many years the probability of cold spells when canvasbacks likely depend on reserves. I then analysed whether the timing of such cold spells is predictable enough to form the basis for monthly schedules of endogenous reserve regulation in free-ranging canvasbacks.

3. Based on 41 years of data, probabilities of cold spells are higher at more northern sites. However, the timing of cold spells of different durations is not predictable at any latitude, providing little selective basis for genetic, time-dependent regulation of reserves on a monthly basis.

4. In North Carolina in 1983–84, the probability of surviving periods of fasting, as calculated from energy reserves and respirometry, decreased more than the probability of cold spells in midwinter, and less than the cold-spell probability in late winter. This suggests that reserves were not successfully regulated to maintain relatively constant mortality risk. Widely varying body mass patterns among years, and higher reserves at some southern sites than northern sites, indicate that canvasbacks maintain greater reserves if proximate conditions allow.

5. Mating and migration systems of many diving ducks (*Aythya* spp.) may disrupt genetic adaptation to specific wintering conditions because (i) pairbonds are mostly formed during spring migration so that mates have often wintered in different areas, (ii) offspring disperse to diverse wintering sites often different from those of their parents, and (iii) ducks often move long distances during winter in response to weather.

6. This analysis provides little evidence that endogenous schedules of nutrient reserves can be effectively tuned to monthly probabilities of cold spells at particular latitudes. Despite evidence for endogenous regulation in captive birds, it appears that free-ranging canvasbacks attempt to maintain high reserves throughout winter within constraints of proximate conditions.

Key-words: body composition, canvasback, cold spells, phenology, nutrient reserve regulation.

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Introduction

Body mass and composition of wintering birds often vary with season, sex and age (Raveling 1979; Nolan

& Ketterson 1983; Whyte & Bolen 1984; Maron & Myers 1985; Baldassarre, Whyte & Bolen 1986; Tietje & Teer 1988; Morton, Kirkpatrick & Vaughan 1990). However, it is often unclear whether nutrient reserves reflect proximate (current) weather and food conditions, or rather endogenous set-points that change through the year due to evolutionary

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adaptation to probabilities of needing reserves at different times (Dugan *et al.* 1981; Reinecke, Stone & Owen 1982; Mortensen & Blix 1985; Dawson & Marsh 1986; Perry *et al.* 1986; Thompson & Baldassarre 1990). With proximate (exogenous) influence, larger reserves suggest that nutrients during the current year are not limiting, i.e. food is abundant relative to need. With endogenous influence, greater reserves indicate that in many years nutrients are limiting during that period, but perhaps not in the current year. Because food availability is difficult to quantify over the large foraging ranges of birds, it is usually also difficult to distinguish these mechanisms. Therefore, despite extensive documentation of body mass and composition for a variety of species, possible implications of these data are often directly conflicting (Pienkowski, Lloyd & Minton 1979; Maron & Myers 1985).

Endogenous regulation has been invoked to explain maintenance of natural weight cycles in captive birds fed *ad libitum* (Mortensen & Blix 1985; Hepp 1986; Perry *et al.* 1986; Loesch, Kaminski & Richardson 1992), asynchrony of body mass and food intake patterns (Stokkan, Mortensen & Blix 1986), return to initial weights after weather-enforced fasts (Dugan *et al.* 1981), and weight declines in late winter that seem unrelated to food availability (Thompson & Baldassarre 1990). Nutrient reserves are presumed to be regulated according to the probability of needing reserves at certain times (Pienkowski *et al.* 1979; Baldassarre *et al.* 1986), with regulation occurring on time scales as short as 3 weeks (Dugan *et al.* 1981). The probability of need, however, is seldom if ever quantified. For example, it has been suggested that body mass declines in late winter because cold spells become less probable (Pienkowski *et al.* 1979; Dugan *et al.* 1981), but the lower probability of cold spells might still be high enough to warrant reserves larger than those observed. Energy reserves are often translated into survival times (fasting endurance) and sex−age variations interpreted in terms of starvation risk (Davidson & Evans 1982; Reinecke *et al.* 1982; Whyte & Bolen 1984; Thompson & Baldassarre 1990; Suter & Van Eerden 1992). However, it is difficult to assess the significance of variations in fasting endurance if the probabilities of fasts of different durations are unknown.

For more critical evaluation of set-point effects, the concept of endogenous regulation needs to be clearly defined and its implicit assumptions identified. In this paper, I will analyse whether cold spells and associated periods of fasting, when their probabilities are calculated with reasonable assumptions, are predictable enough to form the basis for monthly schedules of endogenous reserve regulation in wintering canvasbacks (*Aythya valisineria*).

DEFINITION AND ASSUMPTIONS OF ENDOGENOUS REGULATION

Endogenous regulation of nutrient reserves is presumed to act through physiological set-points that change throughout the year, due to evolutionary adaptation to long-term probabilities of needing reserves at different times (see references above). Such needs include the nutrient demands of reproduction, migration, and winter periods when costs of thermoregulation and foraging exceed food intake. This paper will focus on such cases in winter.

Adaptation of endogenous set-points to long-term probabilities of needing nutrient reserves implies that:

1. Instances of need are temporally predictable, so that time-dependent changes in reserves are appropriate and adaptive. Predictability of need determines how finely tuned the schedule of reserve regulation can be. In this context, *predictability* and *high probability* have different meanings that depend on the relative timing of events. For example, there might be a high probability that a weather-enforced fast will occur sometime during an entire winter (high predictability), but exactly when it occurs during that winter is highly unpredictable. In such cases, nutrient reserves should generally be high, but there is no selective criterion for endogenous (versus exogenous) control of temporal variation in those reserves. Conversely, if there is a very low probability of a fast occurring sometime during winter, it is difficult to predict whether a fast will or will not occur in a given year (low predictability). In this case, low nutrient reserves might be a viable strategy in most years. Thus, high nutrient reserves do not correspond to unpredictable conditions, but rather to predictably harsh conditions (cf. Rogers 1987).

2. Because excessive fat probably impairs predator avoidance (Lima 1986; McNamara & Houston 1990) and increases flight costs (see Lovvorn & Jones 1993), it is adaptive to accept some risk in the 'choice' of set-points relative to the probability of need. For example, are reserves regulated to be adequate for 90% of all possible conditions or only 80%? I will call this probability of reserve adequacy (starvation avoidance) the *hedge probability*. This formulation assumes that costs of nutrient storage, such as predation risk at a given fat level, stay the same throughout winter.

On the other hand, the influence of exogenous (proximate) conditions on reserves and survival probabilities depends on:

1. How well individuals can achieve genetically dictated set-points for reserves (with associated hedge probabilities), given current conditions of weather and food availability.

2. The severity of proximate conditions relative to hedge probabilities for current set-points; e.g. if

reserves are regulated to handle 85% of conditions that might occur, are current conditions more severe than 85% of possible conditions?

Sex and age classes may differ both in hedge probabilities (and thus temporal patterns of set-points) as well as in their ability to maintain reserves at those set-points under different conditions.

The relevant time scale for analysing endogenous versus exogenous effects depends on opportunities for replenishing reserves between periods of negative energy balance. If reserves accumulated in late fall must suffice for the entire winter, there will be poor correspondence between reserves and expected need during short periods in early winter. For example, reserves in December would exceed the probability of needing them during that month. In this case (Case 1), the probability of need on a given date should be calculated for the remaining winter period, i.e. a residual probability. Conversely (Case 2), if reserves can normally be replenished between periods of use, there should be closer correspondence between reserves and the probability of need over short periods. If reserves are closely regulated, then either residual (Case 1) or short-term (Case 2) probabilities of starvation should not change appreciably over time. Rather, the purpose of reserve regulation is to keep the probability of starvation at a relatively constant low level.

Moreover, reserves might be a hedge against either extended periods of chronic nutrient deficit or rather discrete, short periods of fasting. Studies of a variety of large birds suggest that short-term fasts are the primary influence on reserve levels and mortality in winter (Fredrickson 1969; Visser 1978; Dugan *et al*. 1981; Davidson & Evans 1982; Nichols, Reinecke & Hines 1983; Whyte & Bolen 1984; Mortensen & Blix 1985; Conroy, Costanzo & Stotts 1989; Suter & Van Eerden 1992). These considerations of the time scale and intensity of reserve use and replenishment do not apply in the same way to small birds such as passerines, which exhibit daily cycles of reserve buildup and use during overnight fasts (Dawson & Marsh 1986; McNamara & Houston 1990).

RATIONALE FOR CANVASBACK ANALYSIS

Captive diving ducks fed *ad libitum* often reduce food intake and activity during very cold weather (Perry *et al*. 1986; Perry, Williams & Obrecht 1989). For example, in Vancouver, British Columbia, captive canvasbacks, redheads (*Aythya americana*), and lesser scaup (*A. affinis*) stopped eating when mean air temperature dropped from 5·3 °C over 6 days (range 3·1 to 7·2 °C) to −5·5 °C in the subsequent 6 days (range −9·1 to −1·8 °C) (J.R. Lovvorn, unpublished data). During this cold spell, the birds generally floated in a thermally conservative 'sleeping' posture and did not attempt to feed; they resumed

normal feeding on a platform above water when daily mean air temperature exceeded 0 °C (daily minimum > −8 °C). Water temperature in the holding ponds was not appreciably lower during the cold period (varying from 2 to 4 °C), so much of the voluntary fasting response probably involved microclimate at the water surface. In wild diving ducks, foraging may become unprofitable when surface microclimate prevents efficient rewarming after body temperature drops during dives in cold water (Bevan & Butler 1992; Lovvorn 1993).

Strong reduction or cessation of foraging has also been reported in wild Canada geese (*Branta canadensis*) when air temperature at sunrise was below −9 °C (Raveling, Crews & Klimstra 1972) and in American black ducks (*Anas rubripes*) at air temperatures below −10 °C (Albright, Owen & Corr 1983). In a review, Paulus (1988) concluded that Anatids usually increase foraging effort as air temperature declines to about 0 °C. Below 0 °C activity is reduced, apparently because energy costs of foraging exceed energy gains (Paulus 1988).

Wild *Aythya* spp. have been observed foraging on days when mean air temperature is below 0 °C (Noseworthy 1981; J.R. Lovvorn, unpublished data). However, concurrent declines in body mass and fat indicate these birds are in substantially negative energy balance (Jones 1982), and they typically leave the area if weather does not improve (Noseworthy 1981). Based on field observations, it is difficult to separate effects of increased thermogenic demands from effects of ice covering productive feeding sites in shallow water (Jones 1982; Lovvorn 1989a). Regardless of the mechanism, *Aythya* spp. appear to rely heavily on nutrient reserves when daily mean air temperatures remain below freezing.

The major food of canvasbacks wintering in the US mid-Atlantic region, *Macoma* spp. clams (Lovvorn 1987; Perry & Uhler 1988), is nonrenewing (no growth or reproduction in winter) and thus predictable in abundance during a given winter (Lovvorn 1989a). Relative to the wide variation in *Macoma* abundance between winters (Lovvorn 1989a), within-winter changes in the probability of need for reserves should depend mainly on probabilities of weather conditions under which foraging is unprofitable (including ice over shallower feeding sites) and the birds rely on nutrient reserves. This situation allows analyses of canvasback nutrient reserves relative to the probability of fasts of varying duration.

In this paper, I examine differences in body composition among sex and age classes of canvasbacks wintering in North Carolina, and the frequency and predictability of periods when mean air temperature falls below 0 °C based on 41 years of weather data. I then develop an approach for discriminating endogenous versus exogenous effects on body mass

and composition observed in the field. This method involves examining the time course of survival probabilities for different sex and age classes, based on reserve levels in different months and probabilities of fasts of varying duration. Then, by comparing body mass patterns and the frequency and predictability of cold spells at a range of wintering latitudes, and considering the interchange among wintering and breeding populations, I evaluate the relative importance of endogenous versus exogenous effects on nutrient reserves of free-ranging canvasbacks in winter.

Methods

BODY COMPOSITION

Canvasbacks arriving in North Carolina in early November concentrate on Lake Mattamuskeet, and in December move 5−45 km away to Pamlico Sound until departing north mostly in March. Canvasbacks were collected in coastal North Carolina 3−17 November and 21 November to 2 December 1982−83 on Lake Mattamuskeet; and 14−16 December 1983, 12−30 January 1984, and 6−19 February 1983−84 on Pamlico Sound (Rose and Swanquarter Bays). They were also collected at Long Point Bay on the north shore of Lake Erie from 7 March to 10 April 1984. Canvasbacks were shot from shorelines on Pamlico Sound and Lake Erie, and from shorelines and from a small floating blind 1 to 2 km from shore on Lake Mattamuskeet. Carcasses were frozen for later processing. Partially thawed carcasses were sheared of feathers, sawed into smaller pieces, and homogenized in a commercial meat grinder. Duplicate 40−50 g samples of the homogenate were oven dried at 60 °C, combined and ground in a Waring blender, and subsampled in triplicate (3−4 g each) for Soxhlet extraction with ethyl ether. Two 3-g samples of the dried homogenate were ashed for 12 h at 550 °C. Protein content was calculated as the difference between lipid-free dry mass and ash.

For some analyses, I corrected body protein for structural size (see Ankney & Afton 1988). Five structural parameters were considered: keel length (exposed during dissection), culmen length (from the notch at the dorsal base of the bill to the bill tip), tarsus length (from outside the tarsal-metatarsal joint to outside the tarsal-phalangeal joint when flexed at right angles), wing chord (from tip of longest primary to the joint at the wrist), and total length (from tip of bill to tip of tail with the bird flat on its back, minus tail length). I performed principal component (PC) analysis of the correlation matrix for these variables for all sexes and ages combined. Each variable had a positive loading (0·41−0·45) on the first principal component (PC_1); eigenvalues for PC_1 explained 62% of total variance. I used PC_1 scores for each bird as a measure of body

size. Regression of body protein PR on PC_1 scores yielded the equation $PR = 219·9 + 8·11PC_1$ ($r^2 = 0·33$, $P < 0·001$). Protein adjusted for structural size, PR_a, was then calculated as $PR_a = PR − (219·9 + 8·11PC_1) + 220·1$, where 220·1 is the overall mean of PR ($n = 301$). Correlation of body fat with PC_1 scores was negligible ($r^2 = 0·03$, $P < 0·01$), so fat was not corrected for structural size.

BODY MASS AT DIFFERENT LATITUDES

Body masses of canvasbacks trapped in the Maryland portion of Chesapeake Bay from 1972−77 were taken from Perry (1985, p. 47) ($n =$ mean of 135, range 24−472, per sex−age class per month). These birds were not consistently allowed to dry and eliminate digesta before weighing, causing some error (in Maryland, ingested corn at capture averaged about 50 g, Perry 1985, p. 24). Body masses from North Carolina and Lake Erie (see above) do not include digesta. Body masses of canvasbacks trapped on Seneca Lake, New York, where conditions are extreme and sometimes prohibit wintering, were taken from Kaminsky & Ryan (1981). Years of published data were 1972 for adult males ($n = 63$), 1975 for juvenile males ($n = 212$), and 1976 for adult females ($n = 55$) and juvenile females ($n = 68$). Central New York is not an important wintering area for canvasbacks: during years of Kaminsky & Ryan's study (1972−76) about 1000 wintered on Seneca and nearby Cayuga Lakes (R.A. Ryan, personal communication). Maryland, North Carolina, and Louisiana each support at least 30 000 wintering canvasbacks (Lovvorn 1989a; Woolington & Emfinger 1989).

WEATHER ANALYSES

Daily mean temperatures (average of daily maximum and minimum) were obtained from Local Climatological Data available from the National Climatic Data Center (Asheville, North Carolina). I used data from Baltimore, Maryland; Cape Hatteras, North Carolina; and Baton Rouge, Louisiana. Long-term probabilities of cold spells of different durations were calculated as the frequency of periods of varying duration with consecutive daily mean temperatures ≤ 0 °C from 1950 to 1991.

Predictability of cold spells of different durations was assessed in two ways. First, I divided December through February into 10-day periods, calculated the mean temperature for each 10-day period in each year, and then calculated correlation coefficients between mean temperatures in successive 10-day periods (lag of 1) and between periods separated by 10 days (lag of 2; $n = 41$ years). I plotted these coefficients to reveal whether 10-day temperatures can be anticipated from temperatures preceding them in the short or long term (lag 1 or lag 2),

and if such within-year predictability changes with time over winter. These analyses evaluated the potential effectiveness of plastic phenotypic adjustments of nutrient reserves in anticipation of weather patterns predicted over short periods within years, as opposed to genetic regulation of reserves based on long-term, multi-year weather patterns. A period of 10 days was chosen arbitrarily as being long enough to dampen effects of daily weather fluctuations, but short enough to separate within-year, short-term weather patterns from among-year, seasonal weather trends (see Myers & Pitelka 1979). Ten days was also the approximate limit of fasting endurance estimated for several duck species in the wild (Reinecke *et al.* 1982; Suter & Van Eerden 1992) and measured in five captive canvasbacks (mean of 11·5 days, Longcore 1963). Secondly, I calculated predictability, constancy and contingency (Colwell 1974; see Results for definitions) to compare the predictability of cold spells of different durations in different months.

FASTING ENDURANCE

Levels of body nutrients at which starvation-related mortality occurs will vary somewhat with environmental conditions and activities of the birds, and are probably higher in the field than among captives (e.g. from predation on weakened individuals). Among wild birds found starved to death during cold spells, tufted ducks (*Aythya fuligula*) and common pochards (*Aythya ferina*) contained 0·5–0·6% fat (Jenni-Eiermann & Schifferli 1989), and Eurasian coots (*Fulica atra*) contained 3·8–6·1% fat and 24·5–25·7% protein including feathers (Visser 1978). Three canvasbacks I collected in very poor condition that were flying or swimming apart from flocks contained 8–50 g (0·1–5·6%) of fat and 192–210 g (20·0–21·5%) of protein adjusted for structural size (PR_a, see above; these abnormally-behaving birds were excluded from other analyses). I calculated available energy reserves for each canvasback collected based on assumed starvation levels of 15 g of fat and 190 g of structurally-adjusted protein, and energy equivalents ($kJ\,g^{-1}$) of 39·57 for fat and 23·66 for protein (Ricklefs 1974; p. 155).

Oxygen consumption of captive-reared canvasbacks fasted for 12 h and resting in the dark on water at 0–5 °C varied greatly around a mean of $14\,W\,kg^{-1}$, with no significant difference between three males and three females averaging 1052 and 962 g, respectively (Takekawa 1987). Canvasbacks fasting under natural conditions might lower metabolic rate by decreasing body temperature (Chaplin, Diesel & Kasparie 1984). However, fasting metabolic rate in the field would also be elevated by convective heat loss, by swimming to maintain position in wind and waves, and by flying to avoid avian predators and humans (Lovvorn 1989b; Kahl 1991). In the shallow

waters used by canvasbacks in North Carolina, water temperatures closely track air temperatures (J.R. Lovvorn, unpublished data). At water and air temperatures of 0–5 °C, estimated metabolic rate while fasting of $14\,W\,kg^{-1}$ yields a daily energy expenditure (DEE) of $1210\,kJ\,kg^{-1}\,day^{-1}$. I estimated fasting endurance by dividing available energy reserves (see above) by this DEE.

STARVATION PROBABILITIES

I calculated starvation probabilities for canvasbacks in North Carolina in winter 1983–84. I multiplied long-term (1950–91) probabilities of cold spells (fasts) of different durations in different months by the fraction of individuals within a sex–age class with fasting endurance less than those fasting durations. Although captive canvasbacks in British Columbia stopped feeding in very cold weather, this phenomenon is not inevitable in free-ranging canvasbacks at all sites (see above). However, distinct cold spells should closely correspond to periods of dependence on nutrient reserves. The critical point is that if nutrient reserves are regulated over short periods to maintain relatively constant mortality risk, then probabilities of surviving relative to expected conditions over many years (long-term frequencies) should not change substantially over time within winters, even if reserve levels do change. This approach also provides criteria for evaluating the significance of sex–age differences in fasting endurance.

Results

WEATHER AND BODY COMPOSITION IN 1983–84

Air temperatures in North Carolina in 1983–84 were lower than normal in early to midwinter and above normal in late winter (Fig. 1). Following a cold spell in late December 1983 (Fig. 1) fat levels were lower in January (Table 1), although this difference was significant only for adult females. Adults recovered some of their fat reserves in February, but juveniles did not. Body protein increased through winter in all sex–age classes. Within sex–age classes, there were no significant differences among collection periods in lengths of the body, wing chord, culmen, tarsus or keel; in carcass ash content; or in PC_1 scores (Bonferroni multiple comparisons, $P > 0.05$). Thus, seasonal patterns of body composition reflected changes in soft tissues independent of structural size.

BODY MASS AT DIFFERENT SITES

Patterns of canvasback body mass varied substantially among areas (Fig. 2). In the Chesapeake Bay
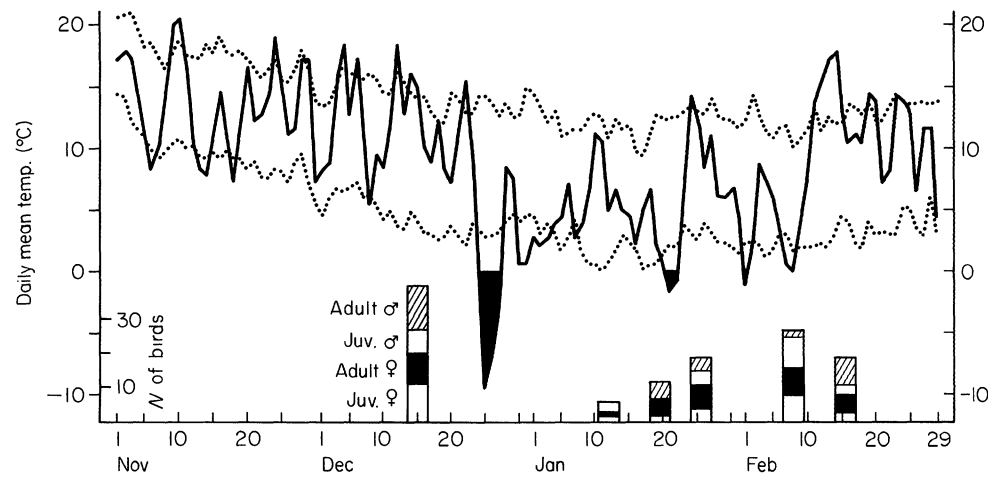
Fig. 1. Daily mean air temperatures at Cape Hatteras, North Carolina, in winter 1983–84, superimposed on the region bounded by ±1 SD for daily mean temperatures from the winters of 1950–51 to 1990–91. Periods when daily mean temperatures fell below 0 °C are shaded. Also shown are numbers of canvasbacks of different sex–age classes collected on different dates in December 1983–February 1984.

of Maryland, body mass of adult females peaked in early winter and declined gradually thereafter, whereas mass in other sex–age classes increased from November to December and remained relatively unchanged for the rest of winter. Body mass in North Carolina generally decreased from November to December, declined further in January after the cold spell in late December (Fig. 1), and either increased, decreased or remained the same in late winter depending on sex and age. In New York,

Table 1. Carcass parameters (mean ± SD, in g) of canvasbacks in North Carolina (November 1982–83 on Lake Mattamuskeet, December–February 1983–84 on Pamlico Sound) and Long Point Bay, Lake Erie (March–April 1984). Within sex-age classes, values not sharing a letter are significantly different (Bonferroni pairwise comparisons, $P < 0.05$).

	n	Body mass	Ash	Protein	Adjusted protein	Fat
Adult male						
Early November	11	1362 ± 135ab	43 ± 6a	221 ± 16a	208 ± 15a	204 ± 63ab
Late November	10	1430 ± 115b	47 ± 5a	230 ± 15ac	215 ± 14ac	283 ± 70b
December	13	1322 ± 97ab	49 ± 4a	239 ± 11ab	222 ± 11ad	189 ± 75a
January	9	1269 ± 75a	47 ± 4a	246 ± 14bc	233 ± 11bcd	132 ± 68a
February	13	1287 ± 54a	48 ± 7a	249 ± 17bc	235 ± 18bd	155 ± 49a
March–April*	26	1274 ± 78a	47 ± 5a	250 ± 16b	239 ± 15b	159 ± 51a
Juvenile male						
Early November	20	1265 ± 100a	42 ± 4a	212 ± 12a	201 ± 13a	185 ± 51ad
Late November	20	1271 ± 113a	43 ± 8a	211 ± 20a	205 ± 15a	202 ± 62a
December	7	1206 ± 121a	44 ± 3a	223 ± 17ac	209 ± 11ac	171 ± 77ac
January	7	1191 ± 56a	42 ± 6a	243 ± 8bc	233 ± 8b	125 ± 32bcd
February	12	1175 ± 83a	45 ± 5a	234 ± 14bc	231 ± 14b	101 ± 50bc
March–April*	8	1220 ± 73a	47 ± 2a	226 ± 15ac	224 ± 12bc	172 ± 58ac
Adult female						
Early November	8	1310 ± 67a	41 ± 5a	201 ± 13a	210 ± 19ad	233 ± 56a
Late November	12	1288 ± 107a	39 ± 3a	200 ± 12a	210 ± 13a	238 ± 77a
December	9	1212 ± 100ac	43 ± 4a	208 ± 9ac	217 ± 10ac	218 ± 82ad
January	13	1137 ± 67bc	43 ± 5a	233 ± 9b	241 ± 12b	125 ± 41b
February	14	1184 ± 68bc	42 ± 4a	225 ± 15bc	235 ± 13bc	145 ± 34bd
March–April*	14	1130 ± 57bc	42 ± 5a	215 ± 17ac	229 ± 14bcd	136 ± 41b
Juvenile female						
Early November	27	1163 ± 78a	36 ± 6a	183 ± 18a	195 ± 17a	181 ± 54a
Late November	11	1125 ± 118a	36 ± 4a	182 ± 13a	197 ± 14a	173 ± 85a
December	11	1139 ± 113a	39 ± 6a	209 ± 19bc	222 ± 13bc	160 ± 88a
January	8	1079 ± 114a	40 ± 4a	220 ± 18bc	237 ± 11bc	133 ± 61a
February	11	1119 ± 60a	39 ± 4a	220 ± 10bc	236 ± 11bc	127 ± 46a
March–April*	2	1025 ± 2a	41 ± 1a	203 ± 13ac	216 ± 7ac	83 ± 24a

* There were no significant differences between paired and unpaired adult males ($n = 6$ versus 13) or females ($n = 8$ versus 6) (t-tests, $P > 0.05$). No juveniles were paired. See Lovvorn (1990) for pair status criteria.

Fig. 3. Means and variances of daily mean air temperatures over 10-day periods at Baltimore, Maryland (open circles), Cape Hatteras, North Carolina (solid circles), and Baton Rouge, Louisiana (triangles), 1950–91 ($n = 41$ winters).
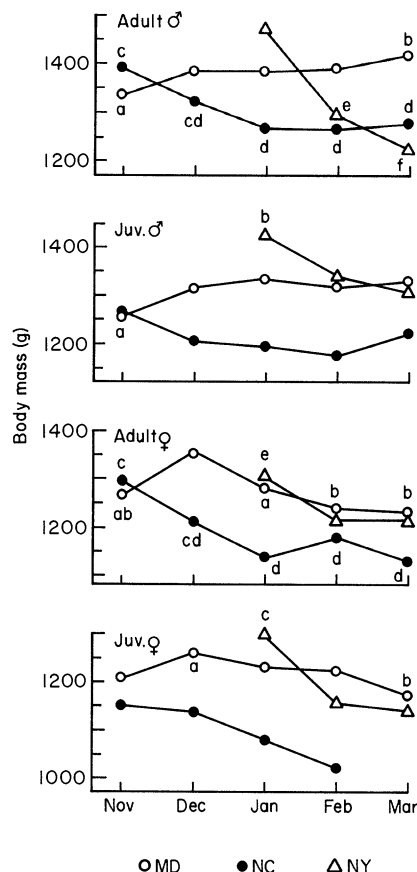
Fig. 2. Mean body masses of canvasbacks in the Maryland portion of Chesapeake Bay (open circles, Perry 1985, p. 47); North Carolina (November–February) and Lake Erie (March–early April) (solid circles, this study); and Seneca Lake, New York (triangles, Kaminsky & Ryan 1981). See text for specific sites, dates, and sample sizes. Within sites, points with different letters, or with letters versus without letters, are significantly different (Bonferroni pairwise comparisons, $P < 0.05$).

body mass declined dramatically from January to February and March. Few canvasbacks winter in central New York, so conditions there have minimal effect on traits in the population as a whole. Nevertheless, the data from New York emphasize the importance of exogenous influences on body mass. During migration in March and early April, body mass in interior New York was either lower or higher than in nearby Lake Erie depending on sex–age class (Fig. 2). In another study at Catahoula Lake and the Mississippi River Delta in Louisiana, canvasbacks collected by shooting from November 1987 through February 1988 were fatter in late winter than canvasbacks I collected in North Carolina (Hohman, Woolington & DeVries 1990).

PROBABILITY AND PREDICTABILITY OF COLD SPELLS AT DIFFERENT LATITUDES

Daily mean air temperatures at major canvasback wintering areas corresponded to latitude, with Maryland being much colder than the other two sites
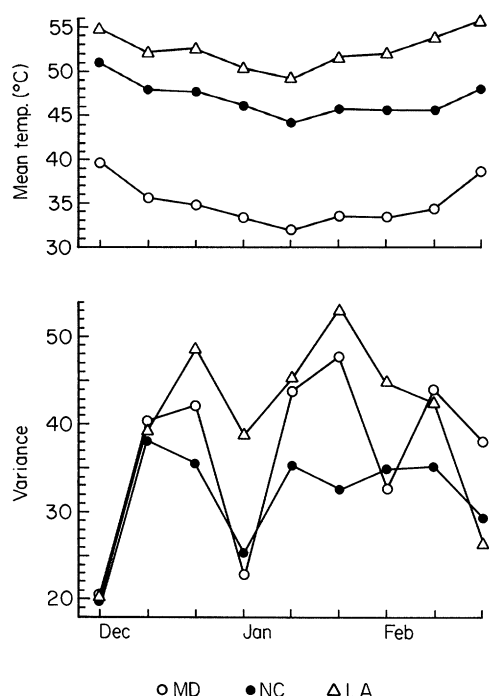
(Fig. 3). Among-year variance in mean temperature tended to be lowest in North Carolina and highest in Louisiana. Variance in all areas was low and similar among sites in early December, and highest in late December and late January.

Air temperatures in North Carolina not only had the highest predictability (lowest variance) among years (Fig. 3), but also were often predictable from one 10-day period to the next within years (Fig. 4a). Within-year, short-term predictability of temperatures (Fig. 4a) was much less consistent in Maryland and Louisiana. Temperatures could very seldom be predicted 20 days in advance at any site (Fig. 4b).

The long-term frequency of cold spells of all durations was generally greater in January than in December or February at all three wintering areas (Fig. 5). Cold spells were far more frequent in upper Chesapeake Bay (Maryland) than at the other sites. Cold spells lasting over 3 days were rare in North Carolina and almost never occurred in Louisiana.

By the formulas of Colwell (1974), in this analysis *constancy* measures the tendency of cold spells to be of a certain duration (e.g. 2–3 days versus longer) regardless of month. *Contingency* represents the degree to which the frequency of cold spells of different durations depends on month (December, January or February). *Predictability*, the sum of constancy and contingency, is the degree to which cold spells in a given month tend to be of a particular duration. Predictability of cold spells shorter than 4 days was significant in both Maryland and North Carolina (Table 2), because most cold spells in all
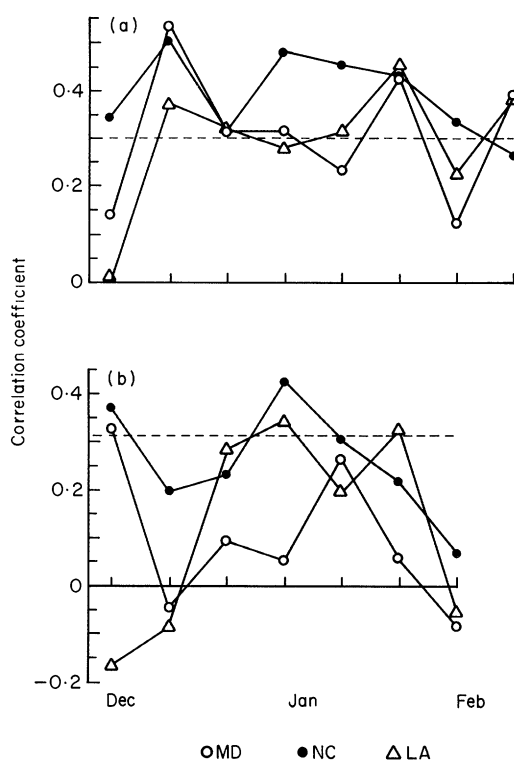
Fig. 4. Correlation coefficients between the average of mean daily air temperatures over 10-day periods versus the means in (a) subsequent 10-day periods (lag 1) and (b) 10-day periods an additional 10 days later (lag 2) in Maryland (open circles), North Carolina (solid circles), and Louisiana (triangles), 1950–91 ($n = 41$ winters). Points above the dashed lines are significantly different from zero ($P < 0.05$).

Table 2. Predictability, constancy and contingency (Colwell 1974) of cold spells (consecutive days with daily mean temperature $\leq 0\,^{\circ}C$) in canvasback wintering areas, December–February 1950–91

	Cold spell duration (days)	Maryland	North Carolina	Louisiana
Predictability	≥2	0·37*	0·58*	0·11
	≥3	0·34*	0·56*	0·21
	≥4	0·31*	0·68	1
Constancy	≥2	0·34*	0·50*	0·08
	≥3	0·30*	0·30*	0·15
	≥4	0·25*	0·33	1
Contingency	≥2	0·03	0·08	0·03
	≥3	0·04	0·26	0·06
	≥4	0·06	0·35	0

* G-test, $P < 0.05$.

3 months lasted only 2–3 days (high constancy; Fig. 5). Longer cold spells were rare and unpredictable in North Carolina. Although the most common duration of cold spells in all months was 2–3 days, cold spells of different durations were equally likely to occur in any month, as shown by non-significant contingency values (Table 2). Cold spells in Louisiana were rare, unpredictable and of very short duration.
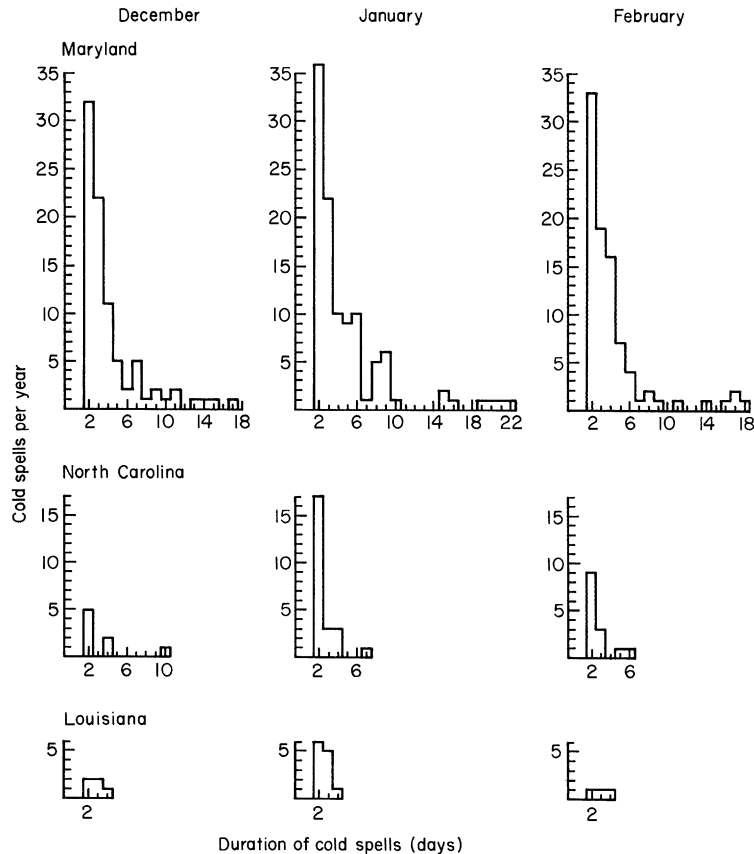

Fig. 5. Number of cold spells (periods with consecutive daily mean temperatures $\leq 0\,^{\circ}C$) per year in canvasback wintering areas, 1950–91 ($n = 41$ winters).

STARVATION PROBABILITIES

Mean estimated fasting endurance of canvasbacks in North Carolina ranged from 3 to 6 days, with the variance generally decreasing from December 1983 to February 1984 (Table 3). The lowest mean was in juvenile males in February. Adult females had the greatest fasting endurance, followed by adult males, juvenile females, and juvenile males. Assuming that canvasbacks rely mostly on reserves when daily mean air temperature falls below 0 °C, the probability that reserves would not last through fasting periods varied substantially and inconsistently between months and sex−age classes (Tables 4−7). Juvenile females had a notably high monthly starvation probability in January, and juvenile males in February (Table 7). Note that estimates of fasting endurance (Table 3) and starvation probabilities (Tables 4−7) reflect nutrient reserves in an exceptionally severe winter (Fig. 1), so fasting endurance may have been lower and starvation probabilities higher than usual.

The important point here is that canvasbacks did not regulate reserves to maintain starvation risk at a relatively constant level. Rather, starvation risk increased substantially in January and did not decrease to original (December) levels in February (Table 7). If canvasbacks regulate reserves in December to last the entire winter, then juveniles must regulate their reserves for a much higher level of risk than adults, which seems unwise if food intake is not limiting. These patterns suggest that reserves were strongly influenced by proximate conditions of weather and food availability.

Discussion

Studies of captive ducks, including canvasbacks, strongly suggest some degree of endogenous regulation of nutrient reserves (Hepp 1986; Perry *et al.* 1986; Pattenden & Boag 1989; Loesch *et al.* 1992). However, my analyses provide little evidence that endogenous schedules of reserves in free-ranging canvasbacks can be effectively tuned to monthly probabilities of cold spells at particular latitudes. Wild canvasbacks appear to regulate reserves only in a very general way (i.e. maintain high fat levels in winter when possible), with fluctuations over shorter periods resulting mainly from exogenous conditions. A number of lines of evidence support this conclusion and partly explain it.

First, in order for time-dependent changes in

Table 3. Estimated fasting endurance (in days) of canvasbacks in Pamlico Sound, North Carolina, winter 1983−84

	December			January			February		
	n	$\bar{x} \pm$ SD	Range	*n*	$\bar{x} \pm$ SD	Range	*n*	$\bar{x} \pm$ SD	Range
Adult male	13	4·7 ± 1·6	1·5−6·6	8	4·0 ± 1·4	2·6−6·2	10	4·2 ± 1·6	0·2−6·2
Juvenile male	7	4·4 ± 1·9	1·2−6·5	7	3·7 ± 0·8	2·9−4·9	10	2·9 ± 1·5	0·3−4·4
Adult female	9	5·8 ± 2·0	1·7−7·9	13	4·0 ± 1·1	2·3−5·8	9	4·8 ± 0·7	3·5−5·6
Juvenile female	11	4·5 ± 2·2	1·2−8·9	8	4·3 ± 1·7	1·8−6·1	11	4·0 ± 1·2	1·8−6·4

Table 4. Calculation of starvation probabilities for canvasbacks in North Carolina in December, based on body composition in 1983 and the frequencies (expected values) of cold spells of different durations during 1950−1990

	Duration of fasting period (days)		
	2	4	10
Fasts/year	0·1220*	0·0489*	0·0244
Adult male (*n* = 13)			
% with inadequate reserves	7·69	23·08	100·00
Starvation probability (%)	0·94	1·13	2·44
Juvenile male (*n* = 7)			
% with inadequate reserves	0	28·57	100·00
Starvation probability (%)	0	1·39	2·44
Adult female (*n* = 9)			
% with inadequate reserves	0	22·22	100·00
Starvation probability (%)	0	1·08	2·44
Juvenile female (*n* = 11)			
% with inadequate reserves	9·09	36·36	90·91
Starvation probability (%)	1·11	1·77	2·22

* Does not include fasts of longer duration.

Table 5. Calculation of starvation probabilities for canvasbacks in North Carolina in January, based on body composition in 1984 and the frequencies (expected values) of cold spells of different durations during 1951—1991

	Duration of fasting period (days)			
	2	3	4	7
Fasts/year	0·4146*	0·0732*	0·0732*	0·0244
Adult male ($n = 8$)				
% with inadequate reserves	0	37·50	50·00	100·00
Starvation probability (%)	0	2·74	3·66	2·44
Juvenile male ($n = 7$)				
% with inadequate reserves	0	0	57·14	100·00
Starvation probability (%)	0	0	4·18	2·44
Adult female ($n = 13$)				
% with inadequate reserves	0	15·38	46·15	100·00
Starvation probability (%)	0	1·13	3·38	2·44
Juvenile female ($n = 8$)				
% with inadequate reserves	25·00	25·00	25·00	100·00
Starvation probability (%)	10·36	1·83	1·83	2·44

* Does not include fasts of longer duration.

Table 6. Calculation of starvation probabilities for canvasbacks in North Carolina in February, based on body composition in 1984 and the frequencies (expected values) of cold spells of different durations during 1951—1991

	Duration of fasting period (days)			
	2	3	5	6
Fasts/year	0·2195*	0·0732*	0·0244*	0·0244
Adult male ($n = 10$)				
% with inadequate reserves	7·69	7·69	69·23	84·62
Starvation probability (%)	1·69	0·56	1·69	2·06
Juvenile male ($n = 10$)				
% with inadequate reserves	33·33	33·33	100·00	100·00
Starvation probability (%)	7·32	2·44	2·44	2·44
Adult female ($n = 9$)				
% with inadequate reserves	0	0	71·43	92·86
Starvation probability (%)	0	0	1·74	2·27
Juvenile female ($n = 11$)				
% with inadequate reserves	9·09	9·09	81·82	90·91
Starvation probability (%)	2·00	0·67	2·00	2·22

* Does not include fasts of longer duration.

Table 7. Overall starvation probabilities for fasts of all durations (sums of values from Tables 4—6) for canvasbacks in North Carolina, winter 1983—84. Residual starvation probabilities for the remaining winter are in parentheses

	December	January	February	Total
Adult male	4·51 (19·35)	8·84 (14·84)	6·00	19·35
Juvenile male	3·83 (25·09)	6·62 (21·26)	14·64	25·09
Adult female	3·52 (14·48)	6·95 (10·96)	4·01	14·48
Juvenile female	5·10 (28·45)	16·46 (23·35)	6·89	28·45

reserve set-points to evolve, the probability of needing reserves must change in a predictable way. There can be little directional selection in a random environment. Probabilities of cold spells are higher in more northern areas (Fig. 5), but the timing of cold spells of different durations is not predictable at any site (non-significant contingencies, Table 2). In North Carolina, temperature can to some extent be

predicted 10 days in advance from current temperatures, but this ability is limited at the other areas (Fig. 4). Therefore, cold spells generally cannot be predicted over the short term to allow plastic, phenotypic changes in nutrient reserves in anticipation of cold spells. Moreover, because the timing of cold spells is inconsistent and unpredictable among years, there is little basis for specific time schedules of endogenous reserve regulation. Depending on site and opportunities for replenishing reserves between cold spells, canvasbacks should either maintain high reserves throughout winter, or else (e.g. in North Carolina) adjust their reserves based on current conditions which predict those over the next 10 days. Neither of these strategies involves monthly schedules for endogenous regulation of reserves during winter.

Increased monthly starvation probabilities in mid-winter for adults and throughout winter for juveniles (Table 7) suggest that reserves declined more than the probability of need. There is no obvious reason that higher risk of starvation should be more or less acceptable in mid to late winter than in early winter, if the goal is to survive the entire winter. I believe that declining survival probabilities, apart from simply declining reserves, resulted mostly from exogenous nutrient limitation. This analysis demonstrates the importance of quantifying the probability of need before assuming that reserve levels simply track such probabilities.

If reserve levels were a direct function of the probability of need, then reserves should increase with increasing latitude (Figs 3 and 5). In years and areas studied, this pattern was evident in New York, Maryland and North Carolina in early to mid winter, but there was no consistent pattern later in winter (Fig. 2). Canvasbacks wintering in Louisiana, where food is abundant and weather quite mild (Hohman *et al.* 1990; Figs 3, 5), were fatter in mid to late winter 1988 than those I collected in North Carolina in 1984 (Hohman *et al.* 1990). This suggests that in some cases canvasbacks are fatter where the probability of need is less, and that canvasbacks maintain greater reserves when exogenous conditions allow. Large annual variations in the magnitude and chronology of winter weights of redheads in New York (Ryan 1972), northern pintails (*Anas acuta*) in California (Miller 1986), and northern shovelers (*A. clypeata*) in coastal Texas (Tietje & Teer 1988) further attest to the dominant effects of exogenous conditions on reserves in free-ranging ducks.

The mating and migration systems of diving ducks may disrupt genetic fixation of set-points for weather regimes in specific areas. Diving ducks (Aythyini) generally select their mates during spring migration (Lovvorn 1989b, 1990) at stop-over sites used by individuals from very different wintering areas. For example, band returns and colour-mark sightings indicate that large numbers of canvasbacks wintering at sites as diverse as Ontario, Maryland, and Louisiana use staging sites on the upper Mississippi River near La Crosse, Wisconsin (Serie, Trauger & Sharp 1983), where much courtship occurs (Lovvorn 1989b, 1990). Thus, mates probably often winter in very different areas (e.g. Louisiana versus Michigan). In turn, offspring disperse to widely varying wintering sites: of canvasbacks banded on breeding grounds in Alberta, 28% of recoveries were from the mid-Atlantic Coast (Maryland to North Carolina) and 48% from the Pacific Coast (Washington to California) (Stewart, Geis & Evans 1958). Therefore, wintering conditions experienced by juveniles probably often differ from those of their parents and siblings. Moreover, canvasbacks and other ducks (Ridgill & Fox 1990) frequently change sites during winter in response to weather; e.g. numbers of canvasbacks in North Carolina increased from 31 000 to 42 000 in mid-February 1983 after a severe weather event to the north in Chesapeake Bay (Lovvorn 1989a).

Thus, differences in mating and migration systems, as well as varying sensitivities of different food types and foraging modes to weather (Davidson 1981), might explain much interspecific variation in the degree of endogenous regulation. In canvasbacks, it is unclear how set-points for more than very gross patterns of nutrient reserves could be selected for (see King & Mewaldt 1981 for discussion of similar conclusions for white-crowned sparrows, *Zonotrichia leucophrys*). These arguments do not preclude the existence of endogenous reserve regulation, but do suggest that such control cannot be effectively tuned to monthly probabilities of cold spells in winter.

Hedge probabilities for fasting endurance in canvasbacks appear to be about 95%, i.e. in early winter they carry reserves adequate to survive 95% of weather conditions they might encounter in the short term (Table 7). However, this hedge probability is not or cannot be maintained at all times (Table 7), resulting in greater starvation risk especially for juveniles. This suggests that birds might not always be able to achieve reserves dictated by endogenous set-points. Such energy limitation might confound field tests for models of body mass as a trade-off between starvation and predation risk (Lima 1986; McNamara & Houston 1990), because reserve levels achieved might not conform to what is optimal.

CRITICAL ASSUMPTIONS AND FUTURE WORK

In this paper, I have evaluated the idea that monthly schedules of nutrient reserves in canvasbacks are endogenously regulated according to long-term probabilities of energy deficit during cold spells. Critical assumptions in my approach are that canvas-

backs rely strongly on stored reserves when daily mean air temperature falls below 0°C, and that energy balance remains non-negative at higher temperatures. Foraging behaviour is difficult to monitor in North Carolina and Chesapeake Bay where canvasbacks feed mostly at night during winter (Lovvorn 1989b; Howerter 1990). However, a number of studies on captive and free-ranging birds suggest that these assumptions are generally valid (Fredrickson 1969; Visser 1978; Dugan *et al.* 1981; Davidson & Evans 1982; Jones 1982; Nichols *et al.* 1983; Whyte & Bolen 1984; Mortensen & Blix 1985; Paulus 1988; Conroy *et al.* 1989; Suter & Van Eerden 1992). Moreover, solar radiation and especially wind speed will alter effects of air and water temperatures, and studies of microclimate, thermoregulation, and foraging efficiency are needed to assess energy balance under diverse field conditions (Lovvorn 1993).

Acknowledgements

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