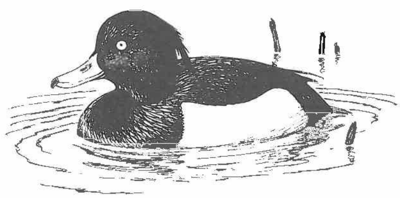
Body mass dynamics of wintering Tufted Duck *Aythya fuligula* and Pochard *A. ferina* in Switzerland



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Using body mass as an indicator of body condition, data from 2973 wintering Tufted Duck and 1335 Pochard trapped at Lake Sempach or shot at Lake Constance were compared and analysed with respect to sex, age, year, seasonal trends, temperature and sites. Throughout the season, males were heavier than females in both adult and first-year age classes, and adults were heavier than first-winter birds of the same sex. Age-related differences were retained throughout winter. Only minor differences were found between years. Body mass of Pochard at Lake Sempach and of female Tufted Ducks at Lake Constance decreased with decreasing ambient temperature. Seasonal patterns differed markedly between the two wintering sites according to feeding conditions and food availability. Diving ducks were able to keep their body mass constant until January or February at Lake Constance, while at Lake Sempach population means of body mass peaked in December when feeding conditions were favourable, and clearly dropped during mid and late winter when feeding conditions were poor. Here, body mass changes of individual ducks suggested a quick adaptation to low site-specific values. This rapid weight loss might reduce survival probability or might force ducks to change wintering sites. Body mass dynamics reflecting habitat quality provide strong evidence that diving ducks attempt to keep body weights as high as possible throughout the winter, and that energy reserves are controlled mainly by proximate factors superimposed on endogenous regulation.

Keywords: Tufted Duck, Pochard, Body Mass, Winter, Sex, Age, Habitat Quality.

Winter, with temperatures below freezing point and limited food resources, is a crucial period in the life of diving ducks. Overwinter survival may depend upon energy reserves to cope with food shortages and increased thermoregulatory demands during harsh weather conditions. Body mass is correlated positively with fat reserves in Redheads *Aythya americana* (Bailey 1979) and Canvasbacks *A. valisineria* (Serie & Sharp 1989, Hohman 1993). It can be considered a good indicator of body condition. For Canvasbacks, body mass combined with season and sex-age classes are the most important variables for the estimation of body condition (Sparling *et al.* 1992). Haramis *et al.* (1986) showed that birds with a relatively high body mass and good body condition in early winter had a higher probability of surviving the winter and the following year. Data for American Black Ducks *Anas rubripes* are ambiguous: Krementz *et al.* (1989) did not find a positive relation between late-winter body mass and annual survival, but Pollock *et al.* (1989) mentioned a higher probability of adult ducks surviving the winter if they are in good condition at the beginning of the winter. Low nutrient reserves may even affect reproductive success of female Ring-necked Ducks *Aythya collaris* nesting in northern bog marshes characterized by low primary production (Hohman 1986). On the other hand, several studies with captive ducks fed *ad libitum* suggest an endogenously regulated loss of body mass that may increase survival by reducing energetic costs (Perry *et al.* 1986 for *Aythya valisineria*, Loesch *et al.* 1992 for *Anas platyrhynchos*).

Body weights of wintering diving ducks have been collected from several North American species (Bellrose & Hawkins 1947, Weller 1957, Ryan 1972, Haramis *et al.* 1986, Perry *et al.* 1986, Hohman *et al.* 1988, Hohman 1993) while comparable data for European diving ducks are lacking. Dementiev & Gladkov (1952), Bauer & Glutz von Blotzheim (1969) as well as Cramp & Simmons (1977) summarized all available data, combining them for various sites and months. For Tufted Ducks *Aythya fuligula*, Mlikovsky & Buric (1983) listed data from the literature without commenting on them; they give mean values for each sex and month, but do not distinguish between

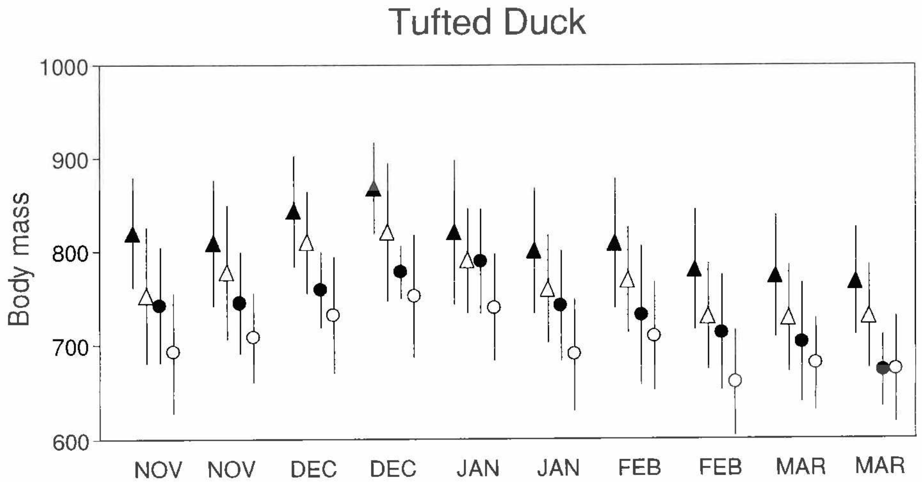

Figure 1. Bi-monthly mean body mass (g) of Tufted Duck trapped at Lake Sempach (± standard deviation). Full triangles = adult males, open triangles = first-year males, full circles = adult females, open circles = first-year females.

Table 1. Bi-monthly mean body mass (g) of Tufted Duck trapped at Lake Sempach (± standard deviation), sample size, minimum and maximum.

	1-15 Nov	16-30 Nov	1-15 Dec	16-31 Dec	1-15 Jan	16-31 Jan	1-15 Feb	16-29 Feb	1-15 Mar	16-31 Mar
ad M	**819**±60 *n*=51 680-950	**809**±67 *n*-44 650-950	**843**±59 *n*=27 710-910	**868**±49 *n*=27 765-1015	**821**±77 *n*=77 650-975	**801**±67 *n*=85 620-955	**809**±69 *n*=56 660-995	**781**±64 *n*=128 625-975	**774**±65 *n*=83 600-915	**768**±57 *n*=30 630-920
juv M	**753**±72 *n*=65 560-910	**778**±71 *n*=123 570-1070	**810**±55 *n*=68 670-940	**821**±74 *n*=67 580-1005	**791**±56 *n*=187 620-925	**760**±57 *n*=161 610-915	**770**±56 *n*=76 625-900	**731**±56 *n*=155 595-895	**729**±57 *n*=110 610-850	**731**±55 *n*=59 600-850
ad F	**742**±62 *n*=19 630-870	**745**±54 *n*=20 625-840	**759**±40 *n*=10 690-800	**778**±28 *n*=5 730=815	**789**±56 *n*=17 680-890	**742**±59 *n*=23 625-850	**732**±74 *n*=26 600-955	**713**±62 *n*=35 595-850	**703**±73 *n*=34 585-830	**672**±39 *n*=12 605-730
juv F	**692**±63 *n*=42 545-870	**708**±47 *n*=38 620-825	**732**±62 *n*=45 570-860	**752**±65 *n*=30 635-870	**740**±57 *n*=117 610-890	**690**±59 *n*=77 580-830	**709**±58 *n*=71 580-835	**660**±56 *n*=153 490-820	**680**±49 *n*=88 575-835	**674**±56 *n*=48 560-825

Table 2. Bi-monthly mean body mass (g) of Pochard trapped at Lake Sempach (± standard deviation), sample size, minimum and maximum.

	1-15 Nov	16-30 Nov	1-15 Dec	16-31 Dec	1-15 Jan	16-31 Jan	1-15 Feb	16-29 Feb	1-15 Mar	16-31 Mar
ad M	**936**±106 *n*=4 830-1080	**997**±78 *n*=28 840-1250	**991**±62 *n*=37 840-1110	**1004**±76 *n*=38 835-1185	**970**±76 *n*=52 720-1110	**946**±70 *n*=67 780-1125	**917**±69 *n*=39 715-1030	**893**±63 *n*=54 720-1035	**888**±60 *n*=28 800-1000	**904**±28 *n*=8 870-960
juv M	**881**±66 *n*=7 790-970	**933**±70 *n*=48 815-1160	**949**±73 *n*=73 780-1060	**1000**±70 *n*=46 880-1155	**957**±69 *n*=78 800-1155	**915**±69 *n*=51 775-1055	**880**±58 *n*=39 755-1020	**858**±52 *n*=54 725-980	**884**±71 *n*=33 750-1120	**899**±74 *n*=13 810-1075
ad F	**859**±91 *n*=6 790-1050	**890**±59 *n*=12 790-995	**921**±57 **n**=7 820-1000	**988**±106 *n*=18 760-1175	**914**±72 *n*=9 790-1030	**913**±75 *n*=15 790-1055	**865**±57 *n*=12 755-940	**869**±38 *n*=27 785-960	**855**±52 *n*=23 740-940	**833**±59 *n*=12 735-905
juv F	**827**±85 *n*=10 650-980	**890**±105 *n*=41 670-1075	**890**±80 *n*=42 730-1050	**954**±79 *n*=21 830-1145	**910**±81 *n*=51 740-1170	**866**±61 *n*=27 730-990	**829**±69 *n*=24 700-950	**806**±58 *n*=46 690-920	**815**±56 *n*=28 720-995	**809**±95 *n*=15 675-1070

Table 3. Monthly mean body mass (g) of Tufted Duck shot at Lake Constance (± standard deviation), sample size, minimum and maximum.

	November	December	January
ad M	**880**±98 n=13 730-1020	**891**±63 n=23 730-980	**845**±73 n=91 690-1030
juv M	**830**±79 n=6 720-930	**769**±66 n=9 690-890	**795**±76 n=74 640-980
ad F	**785**±68 n=7 700-910	**785**±81 n=17 675-925	**799**±64 n=54 670-970
juv F	**748**±114 n=5 600-880	**755**±59 n=25 630-900	**742**±70 n=60 600-870

Table 4. Monthly mean body mass (g) of Pochard shot at Lake Constance (± standard deviation), sample size, minimum and maximum.

	November	December	January
ad M	**1007**±114 n=11 800-1170	**1018**±108 n=23 820-1230	**943**±77 n=26 810-1120
juv M	**955**±128 n=4 820-1100	**966**±126 n=12 760-1225	**870**±81 n=5 790-980
ad F	**938**±86 n=3 870-1035	**950**±77 n=14 800-1050	**832**±96 n=5 710-960
juv F	**1000**±60 n=3 940-1060	**972**±97 n=5 830-1100	**687**±85 n=3 600-770

Table 5. Body mass (g) of adult male Tufted Ducks from various wintering sites.

location	date	mean	s.d.	n	remarks	reference
Lake Zurich	January	1023	54	13		Güntert (1978)
Dutch Waddenzee	Jan-Feb	987	140	82	ad+juv	Suter & van Eerden (1992)
German Baltic coast	Nov-Feb	952	79	8		Piechocki (1987)
Lake Constance	January	891	63	23		this study
Lake Sempach	January	811	73	162		this study
Caspian Sea offshore	January	882	?	?		Dementiev & Gladkov (1952)
Caspian Sea coast	January	717	?	?		Dementiev & Gladkov (1952)
Camargue	January	729	77	100		Bauer & Glutz (1969)

adult and first-winter birds. Data for Pochards *A. ferina* are even scarcer than for Tufted Ducks.

This study compares body weights and their seasonal trends from two different sites. Such differences could point to different survival probabilities among habitats and, therefore, might also support the hypothesis assuming primarily exogenously controlled body mass changes. It is assumed that diving ducks that face unpredictable weather or changing feeding conditions attempt to keep the highest possible body weight throughout winter. Because the timing of cold spells is not predictable (Lovvorn 1994), there is little evidence for genetic, time-dependent regulation of energy reserves in wintering diving ducks.

Material and Methods

Lake Sempach

The hypertrophic Lake Sempach (47°09'N/ 8°07'E, 504 m ASL) in the central Swiss lowlands has a surface of 14.4 km^2. Zebra Mussels *Dreissena polymorpha*, which constitute the main food of diving ducks on most

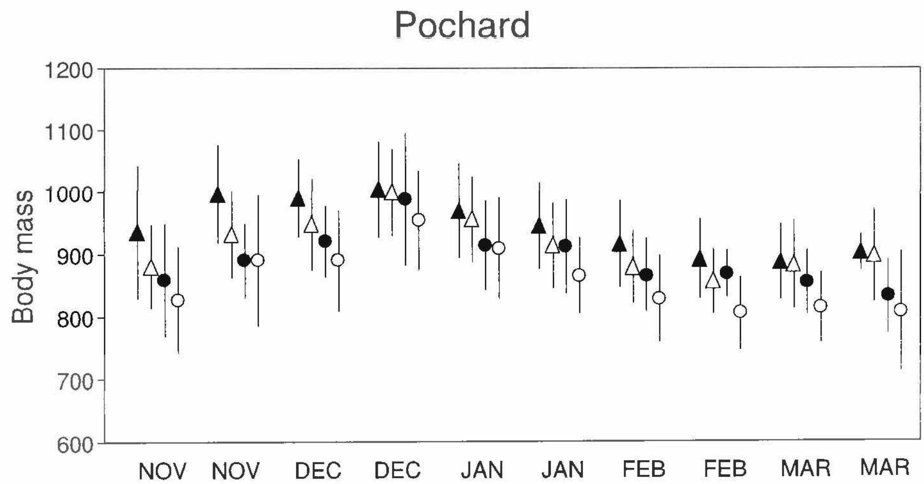

Figure 2. Bi-monthly mean body mass (g) of Pochard trapped at Lake Sempach (± standard deviation). Full triangles = adult males, open triangles = first-year males, full circles = adult females, open circles = first-year females.

Swiss waters, have not yet been recorded (Turner 1984, pers. obs.). Therefore, diving duck populations are small and their food normally consists of small benthic invertebrates and submerged plants, mainly *Potamogeton sp.* In the second half of December, however, numbers of diving ducks increase quickly up to 1500 when the birds are feeding on the spawn of *Coregonus sp.* fish which is temporarily available in large quantities (Kestenholz 1990). As the availability of spawn ceases in early January, numbers of diving ducks decrease rapidly and in mid-January, counts made in 1961-89 averaged 172±132 Tufted Ducks and 75±60 Pochards (Kestenholz 1990). In the winters of 1987-88, 1989-90 and 1990-91, 2589 Tufted Ducks and 1221 Pochards were caught in a wire trap baited with corn and fish offal (Hofer & Marti 1988). The ducks usually entered the trap during the night, were held in bags for 4-6 hours to allow the passage of ingesta (Haramis *et al.* 1982), and released in late morning after being

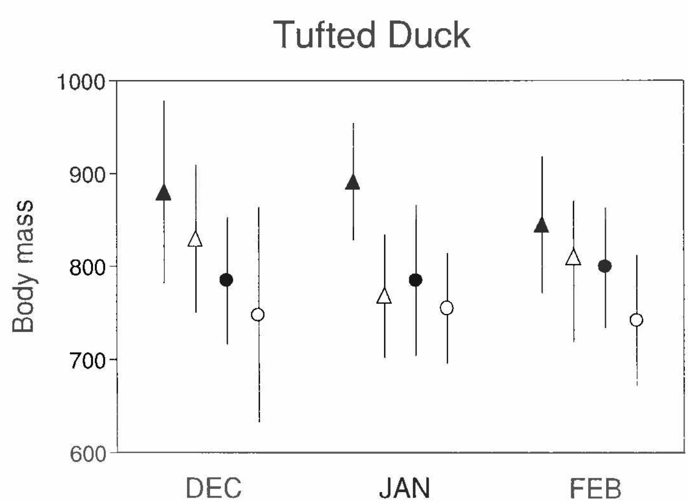

Figure 3. Monthly mean body mass (g) of Tufted Duck trapped at Lake Constance (ñ standard deviation), sample size, minimum and maximum. Full triangles = adult males, open triangles = first-year males, full circles = adult females, open circles = first-year females.

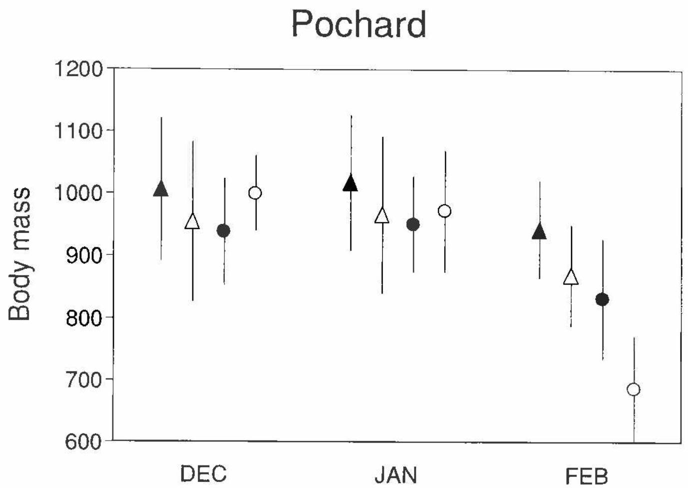

Figure 4. Monthly mean body mass (g) of Pochard shot at Lake Constance (± standard deviation). Full triangles = adult males, open triangles = first-year males, full circles = adult females, open circles = first-year females.

ringed, sexed, aged and weighed to the nearest 5 g. The weights recorded were of unringed birds or of individuals handled for the first time that season in order to avoid bias from repeated captures.

Lake Constance

Lake Constance on the Swiss-German border (7°35'N/9°20'E, 396 m ASL) has an area of 541.2 km^2. Its western part comprises two wintering sites of international importance for Tufted Duck, Pochard,

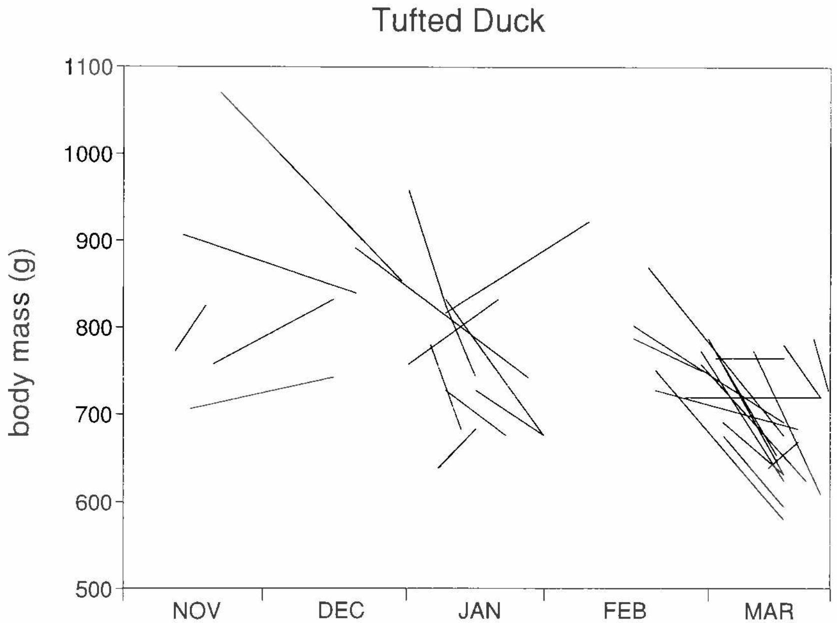

Figure 5. Body mass changes (g) of individual Tufted Duck wintering at Lake Sempach.

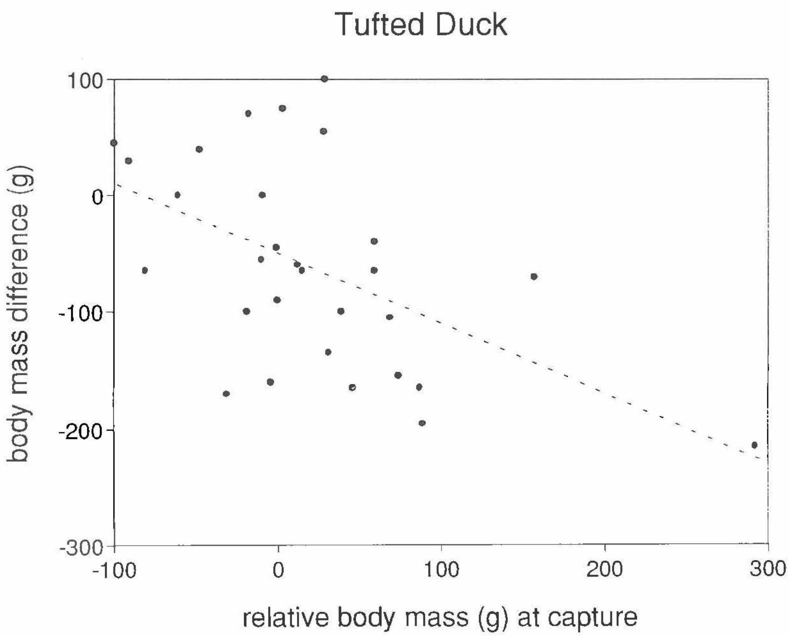

Figure 6. Body mass difference (g) of individual Tufted Duck wintering at Lake Sempach in relation to relative body mass at capture rmC (g). Relative body mass is referring to corresponding population means of sex and age.

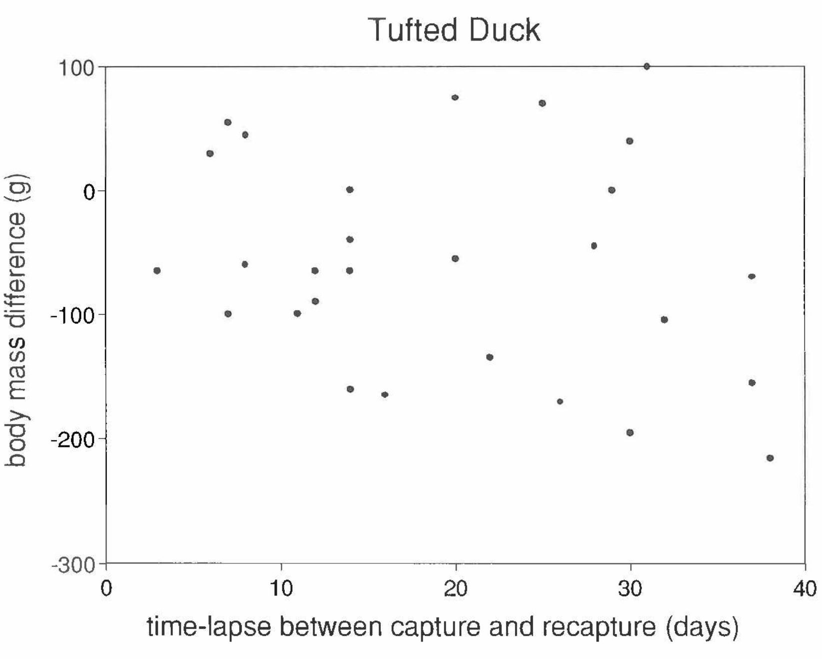

Figure 7. Body mass difference (g) of individual Tufted Duck wintering at Lake Sempach in relation to time-lapse (days) between capture and recapture.

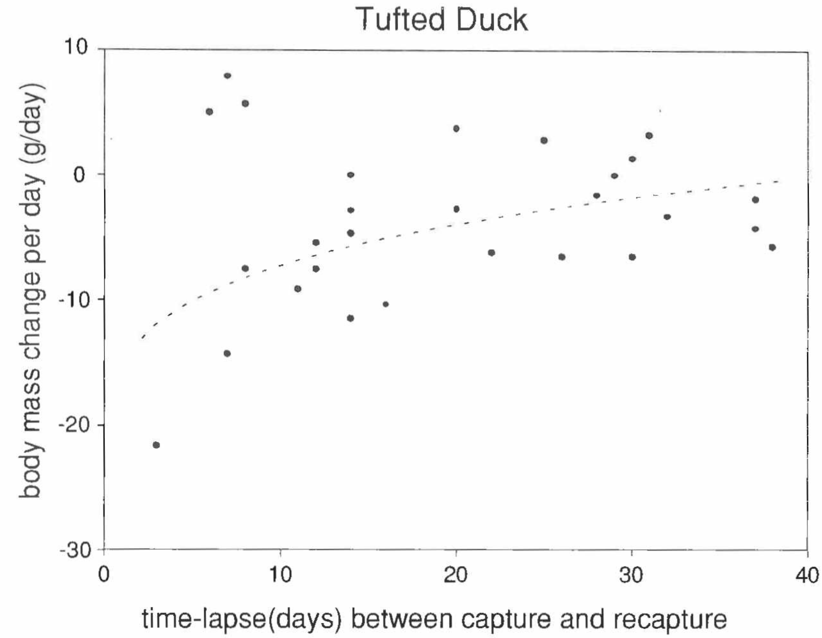

Figure 8. Body mass change per day (g/day) of individual Tufted Duck wintering at Lake Sempach in relation to time-lapse (days) between capture and recapture.

Red-crested Pochard *Netta rufina* and Gadwall *Anas strepera* (Marti & Schifferli 1987). Numbers of diving ducks peak in November (Schuster *et al.* 1983) and decrease to 43,000 Tufted Ducks and 19,000 Pochards in mid-January (averages of 1976-87, Suter 1991). They feed almost exclusively on zebra mussels which have mean densities of 4500 g freshweight / m^2 (Suter 1982). Body masses of 384 Tufted Ducks and 114 Pochards were collected from hunters' bags in 1982-83, 1983-84 and 1984-85 (Meile 1991).

Birds were sexed and aged according to plumage characteristics and these facts were confirmed by cloacal examination if necessary (Bauer & Glutz von Blotzheim 1969). In this paper, first-year or young refers to birds hatched in the preceding breeding season, adult refers to at least one year old birds.

The model using sex, age, year as main effects with sex x age, sex x year, age x year, and sex x age x year interactions and date as a covariate was tested by three-way ANCOVA. Residuals from the analysis of covariance were then examined for possible influences of ambient temperature (daily mean temperature of days 1 to 7 previous to weighing as well as mean temperatures of various combinations of day 1 to 7; best results are given). At Lake Sempach, 29 Tufted Ducks were retrapped up to three times within 40 days. Since mean body mass changed markedly in the course of the winter, relative body weights for capture rm_C and recapture rm_R were calculated as the differences between body mass and the corresponding means (**Figure 1**) of sex, age and season. Statistical tests were carried out using program SPSS/PC+ V2.0 (SPSS Inc., Chicago, 1988).

Results

Body mass

At Lake Sempach, the body weight of Tufted Duck (**Figure 1**) varied by sex (three-way ANCOVA $F_{1,2576}$=672, P<0.001), age ($F_{1,2576}$=141, P<0.001), year ($F_{2,2576}$=7.6, P<0.001) and season (date as a covariable, b=-0.473, P<0,001) without interactions. Weights of Pochards (**Figure 2**) also varied by sex ($F_{1,1208}$=160, P<0.001), age ($F_{1,1208}$=33, P<0.001), year ($F_{2,1208}$=11.8, P<0.001) and season (date as a covariable, b=-0.847, P<0.001) without interactions. For both species, weights peaked in the second half of December and decreased towards February. Effects of years, however, were not significant when sex-age-classes were treated separately.

At Lake Constance, the body weight of Tufted Duck (**Figure 3**) varied by sex ($F_{1,375}$=45, P<0.001), age ($F_{1,375}$=57, P<0.001) and year ($F_{1,375}$=8.4, P<0.01) without interactions. For Pochard (**Figure 4**), similar differences were found for sex ($F_{1,106}$=6, P<0.02) but not for age ($F_{1,106}$=2.6, P=0.11) and year ($F_{1,106}$=0.6, P=0.44). Tufted Ducks kept their body mass constant during winter while Pochard body mass remained constant only from December to January and decreased from January to February.

In December, site-specific differences in body weight of ducks trapped at Lake Sempach and of birds shot at Lake Constance for all sex and age classes were neither recorded for Tufted Duck ($F_{1,307}$=0.8) nor for Pochard ($F_{1,278}$=0.4). In January, and especially in February, Tufted Ducks ($F_{1,2660}$=192, P<0.001) and Pochards ($F_{1,1051}$=31, P<0.001) at Lake Sempach were, however, significantly lighter than at Lake Constance. At both sites, differences between sex and age classes remained throughout the winter.

Influence of ambient temperature

At Lake Sempach, no relationship was found for Tufted Ducks, but Pochards decreased in body mass with decreasing temperature (most significant regression for the sum of means from 5th to 7th days before capture; b=0.621, P<0.001). At Lake Constance, only body weights of female Tufted Ducks were influenced by ambient temperature (most significant regression for the sum of means from day 3 to 5 before capture; b=0.897, P<0.01).

Mass changes of individual Tufted Ducks

Mass changes of individual Tufted Ducks showed large individual differences (**Figure 5**). The average individual loss was 3.2 g/day (n=29). Relatively heavy ducks decreased in body mass while relatively light birds tended to increase their body mass (**Figure 6**). This process reduced deviations from mean values implying that ducks adopted a lake-specific body mass in a few days. Afterwards, relative individual body mass did not decrease further because there was no significant relation between relative body mass difference and staging time (**Figure 7**, r=-0.19, n.s.) but absolute body mass continued to decrease (**Figure 1**). Body mass loss per day was decreased with time-lapse between capture and recapture (**Figure 8**, $y = 14.6\ x^{0.2} - 30$, r=0.42, P<0.05). Therefore, the body mass change started with a steep line that levelled off subsequently. If this initial change had been a reaction upon handling, relative body mass would increase later on which was not the case.

Discussion

Methodical remarks

Comparisons of body mass data from various sites collected by different methods should be interpreted with caution. In practice, it is difficult to obtain a random sample from the population of interest for comparison of trapped with shot birds. Ducks drowned in fishing nets probably best represent the population considered but such birds usually contain a lot of water in their lungs. Capture methods exploiting a feeding response disproportionately sample food-stressed individuals (Weatherhead & Greenwood 1981) but no differences were detected between Mallards *Anas platyrhynchos* caught with unbaited rocket nets (control) and baited traps, but body condition of shot Mallards was below the control sample (Greenwood *et al.* 1986, Reinecke & Shaiffer 1988). If birds are spatially segregated on a local scale, a condition bias might be expected (Dufour *et al.* 1993). At Lake Sempach, both species are sexually segregated with the highest proportion of males at the trap location (Kestenholz 1990). Nothing is known about diurnal mass changes in ducks.

At Lake Constance, with its large areas of shallow water and intense hunting activity, lead pellets were consumed by 12 % of waterfowl including Tufted Duck and especially Pochard (Zuur 1982). This probably affected their weight. Body mass of male Lesser Scaup *Aythya affinis* and presumably female Canvasback is reduced when blood lead concentrations exceed 50 ppm (Havera *et al.* 1992). The body mass of Canvasbacks with lead shot in their gizzards is reduced by 10% (Hohman *et al.* 1990).

Human activities, e.g. water sports and fishing, might also influence body conditions but are not discussed in this paper. Disturbances by hunting may also affect mass negatively. However, in spite of important hunting activity at Lake Constance, masses in December were the same as at Lake Sempach.

Effects of sex and age

For both species, males were heavier than females and adult ducks heavier than juveniles. This corresponds to most other studies (Ryan 1972, Sparling *et al.* 1992) but Hohman (1993) reports that in wintering Canvasbacks females are heavier than males although males are larger, and Gauthier *et al.* (1992) did not find body mass differences between sexes of wintering American Black Ducks which show no clear sexual dimorphism in plumage coloration. At both sites, age differences were retained until late winter. Thus, first-year birds from Switzerland will not attain adult weights before spring or summer, probably causing reduced breeding success because of delayed spring migration, reduced nutritional reserves or failed pair formation. Physical condition as well as reproductive success (clutch size and one-day-old duckling weight) of female Pochards and Tufted Ducks nesting at the Engure Marsh, Latvia, were clearly age-dependent (Blums *et al.* 1985). On the other hand, Ring-necked Ducks wintering in Florida adjust to adult body mass during winter (Hohman *et al.* 1988).

Effects of habitat quality on body mass and seasonal trends

Average body mass and seasonal pattern vary greatly among sites (**Table 5**) suggesting a major influence of habitat quality even if this comparison is very tenuous because of the different sampling techniques. Food availability, winter climate and disturbances (predation, hunting) are among the main factors determining the quality of a wintering site. At Lake Sempach, in December, large quantities of fish spawn offer temporary feeding conditions (Kestenholz 1990) comparable to Lake Constance, and body mass is the same at both sites. But this food resource is available for only a few weeks. As a consequence, body mass drops thereafter. The rapid decrease in food availability results in emigration of most of the diving ducks. Trends of re-trapped Tufted Ducks indicate that body weights quickly adjust to low lake-specific values. By contrast, favourable feeding sites promote accumulation of fat reserves. At Lake Constance, body weights of Tufted Ducks feeding on *Dreissena polymorpha* mussels are constant and significantly higher than at Lake Sempach except for December. These clear differences in body mass and, especially, in seasonal body mass trends fit well with feeding conditions while climate is the same for both sites. Tufted Ducks from the German Baltic coast (Piechocki 1987) are slightly lighter in December and slightly heavier in January than at Lake Constance. Their main food consists of *Mytilus edulis* and *Cardium sp.* mussels. The area of Lake Ijsselmeer and the westernmost part of the Dutch Waddenzee provide even better feeding conditions with important mussel concentrations, mainly *Mytilus edulis.* This major wintering site holds up to 160,000 Tufted Ducks and 50,000 Pochards. Diving ducks freshly drowned in gill nets in February 1980-89 show even higher winter masses (e.g. 987±140 g for male Tufted Ducks, Suter & van Eerden 1992). Highest winter masses of Tufted Ducks (e.g. 1023±54 g for adult males) recorded from Switzerland are those of 41 birds drowned at Lake Zurich in January 1974 (Güntert 1978) where feeding conditions were excellent due to large numbers of Zebra Mussels. Water in the birds' lungs might partly explain these extremely high values, but Güntert (1978) also reported massive fat deposits. Thus, food availability plays a decisive role in regulating body weight; the type of food is much less important (Hohman 1993). Ducks wintering at the most southern sites with a mild winter climate show a constant increase in body mass during winter. In the Camargue, southern France, mean body weights of Tufted Ducks and Pochards increase until February (Bauer & Glutz 1969), Ring- necked Ducks wintering in southern Florida put on fat reserves throughout the wintering period (Hohman *et al.* 1988) and Redheads from two sites in Louisiana also gained body mass during winter (T. Michot, *in litt.*). In northern latitudes, however, body mass of wintering diving ducks normally peak in mid winter and decrease subsequently to reach weight minima in late winter (e.g. Ryan 1972 for *Aythya ameri-*

cana). Therefore, starvation is most likely to occur at the end of the wintering season.

The body mass decrease from mid to late winter was suggested to be an endogenously regulated adaptive reaction to reduce energy costs for maintenance, flight costs and predation risk (Perry *et al.* 1986, Gauthier *et al.* 1992, Loesch *et al.* 1992). Provided that such endogenous patterns are involved, it seems that they are often superimposed the influence of environmental factors and therefore are not always perceptible. The area of the Caspian Sea provides another example of environmentally influenced body weights where flock size seems to be an indicator of habitat quality. Big flocks of Tufted Ducks foraging offshore had higher individual body mass than small groups at the coast (**Table 5**, Dementiev & Gladkov 1952). And for Canvasbacks wintering at different sites in the USA, body mass pattern varying widely among latitudes and years indicate that Canvasbacks maintain greater reserves if proximate conditions allow (Lovvorn 1994).

Diving ducks facing insufficient habitat quality have to change behaviour in order to avoid loss of body condition. Low temperatures could be compensated with increased food intake as long as excellent feeding conditions prevail. For instance, a temperature influence has not been recorded in experiments with captive Mallards fed *ad libitum* (Loesch *et al.* 1992.) or in wild Mallards at profitable feeding sites (Whyte & Bolen 1984). But Lovvorn (1994) observed that Canvasbacks, Redheads and Lesser Scaup *Aythya affinis* reduced or even stopped feeding during very cold weather. Thus, harsh weather or poor feeding conditions may trigger emigration. At Lake Constance, a significant relation between body mass and temperature was found only in female Tufted Ducks, which were the smallest birds considered. At Lake Sempach, an influence of temperature was observed for Pochards but not for Tufted Ducks. Here, the situation is confusing because most ducks are forced to leave the lake as soon as feeding conditions deteriorate. In the worst case, cold spells coinciding with depleted food resources may cause severe mortality. Such a mass starvation of diving ducks was recorded at Lake Constance in late February and March 1986 (Suter & van Eerden 1992).

Body conditions reflecting habitat quality seem to be related to fitness (Haramis *et al.* 1986). Future research, therefore, should focus on annual survival in relation to different wintering locations. This should help to estimate the amount and type of habitat needed to support wintering populations of diving ducks.

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