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Research Article

No Optimal Weight to Survive the Winter in a Northern Island Population of Water Voles *Arvicola amphibius*

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Abstract

Growth and body size of mammals are commonly correlated with many life history strategies, including those related to survival and reproduction. However, in certain circumstances suboptimal growth rates and smaller size may be advantageous and adaptive. The water vole *Arvicola amphibius* is a large vole, about three times the size of a field vole *Microtus agrestis*, but with similar ecological and reproductive characteristics. Island populations were studied on the coast of northern Norway, just below the Arctic Circle, during 2003-2018, by capture-mark-recapture. The main aims were to study growth rates, asymptotic weight and survival, expecting that the "optimal" weight for surviving the winter would be 140-160 g. The smallest juveniles caught weighed only 21 g and were assumed, based on data from the literature, to be around 14 days old. This age was used as starting point for the growth curve. This, however, may have been about one week too early, as juveniles are more likely not fully weaned and leave their nest of birth until 30-40 g. Initial growth rates in juveniles was relatively high but declined from around 100-120 g or 40-50 days old. The asymptotic weight was not clearly defined, but its maximum was around 150-160 g. Most juveniles that survived the winter weighed between 100 and 160 g in their first summer. Large individual variations in growth rates were found. Overwintered subadults in spring weighed about the same as juveniles did in the autumn but grew quickly in April and May to reach adult size. A specific "optimal" weight for juveniles that survived the winter was not found. The range could be given as 100-160 g, too broad to define an "optimal" weight range. However, those that survived tended to be slightly heavier than those that died. Reproducing adults generally weighed 180-220 g and did not reduce their weight toward the autumn, i.e., to increase winter survival, but very few adults survived even the summer and almost none survived their second winter. Juveniles postponed reproduction until next spring, most likely to take advantage of fresh vegetation growth and less competition.

Keywords

Growth Rates, "Optimal" Weight, Survival, Voles, Weight Adjustment

1. Introduction

Growth and body size in mammals are commonly correlated with many life history strategies, including those related to survival and reproduction [1-4]. However, in certain circumstances suboptimal growth rates and smaller size may be advantageous and adaptive [4-8]. Large size can be negatively related to population growth rate and positively related to density [6, 9, 10]. There are trade-offs in the allocation of resources to growth versus other requirements, including predator avoidance, and faster growth rates may incur an extra cost [4, 9, 11, 12]. Various individuals in a population may

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represent different strategies in growth rate and size, and consequently, in reproduction and survival. For example, the “quick and small” may do better under high predation pressure, while the “slow and big” may do better under lower predation pressure (sensu [13]). A highly seasonal environment adds an extra factor that may have consequences for growth and survival, i.e., through variance in the length of the growth period, through reductions in the amount and quality of food over a prolonged time and through changeable predation rates [14].

Microtine rodents (subfamily Arvicolinae) are good role models with respect to all these variables [12]. They are highly affected by season, climate and predators, and often exposed to climate extremes. Population sizes often fluctuate greatly between years, which may be associated with changes in individual characters, including body weight, termed the Chitty effect [6, 9, 10, 12, 15]. The observed variation in body size may follow a trade-off between allocating resources to growth versus reproduction [11, 16]. Such variation can arise from variation in juvenile growth rates or length of growth periods, or from differential survival rates that depend on body size [12]. The variations in and constraints on body size may potentially be integral parts of some species population cycles (the Chitty effect: animals are larger during the increase and peak phases of a population fluctuation cycle). Social dominance and reproductive success are generally associated with larger body size, but not so much survival [6, 8]. In model terms, optimal body mass was defined as the point on the trade-off curve with highest fitness and was negatively associated with energy expenditure [17]. In this study, the energetic costs of maintaining a given body mass in *Microtus agrestis* differed between sites. In *Lasiopodomys brandtii*, a vole that live in groups mainly below ground during the winter, an optimal autumn body weight for surviving the winter was found, with counterbalancing selection between energy conservation and winter survival [18].

The water vole *Arvicola amphibius* is a large species among voles, weighing up to 350 g in Britain [19]. It lives in boreal and seasonal environments and is vulnerable to predation, weather conditions and food availability [20], but shows a remarkable ecological plasticity. About three times the size of a *Microtus* vole, the water vole’s growth and development are of particular interest. Large size may also imply a larger variation in size, and the effects of size on survival and reproduction can be more pronounced.

Large size may also be associated with faster growth rates and the difference in size between subadult and adult water voles is particularly noticeable, and “… juvenile water voles probably need to attain a weight of 170 g in order to survive the winter” [19]. Another study [21] on the other hand, concluded that weight increased up to 100-120 g in non-mature juveniles and stayed at this level until next spring. Larger-sized voles may be socially dominant and able to select better food and shelter, as well as conserve body heat more efficiently, thereby increasing their survival [17]. However, they also need more food that, in turn may expose them more to predators. They may even be more prone to predation risk if predators selectively hunt larger individuals. To survive the winter, a moderate weight may be more ideal and the high and low extremes should be avoided [2, 4, 14].

In this study, I examine growth rates and weights of juvenile and adult water voles in an attempt to find the “optimal” weight for voles to survive the next winter. Is there an “optimal” weight range for survival? The main hypothesis is that juvenile weight would initially increase fast before slowing down to approach an upper asymptote weight. This value would represent the upper level of the “optimal” weight range. To survive the winter at all would require reaching a certain minimum weight in late summer, representing the lower level of the “optimal” weight range. At the end of the reproductive season, adults would reduce their weight to approach the “optimal” weight range, in order to enhance their survival during winter, but their upper and lower limits may be larger than in juveniles. Overall, I hypothesized that a weight around 150 g (140-160 g) would be “optimal” in this population for surviving the next winter. Because storing body fat is not an option, larger water voles may be at a disadvantage, requiring more food and being less agile.

2. Material and Methods

This study was conducted on several small islands in the archipelago of Solvær, Nordland County in northern Norway, just below the Arctic Circle [20, 22]. Live trapping was performed in the summers of 2003-2018. In 2003-2008 voles were trapped at various times from April to October but from 2009 trapping was standardized to two periods: spring (May) and late summer (July-August). Although the late summer trapping session included the last days of July, all these data were assigned to the month August. The summer was divided into two parts: early season=before 24 July and late season=after 24 July.

The study areas were relatively flat fields. No other small mammal lived on these islands, but sheep *Ovis aries* grazed in many of the fields and years [23]. The eagle owl *Bubo bubo* was a stationary and highly significant predator on water voles [20, 24]. New vegetation growth started in May, depending on the temperature, but was not always significant until the end of that month.

The voles were trapped in 36 custom-made single-entry cage traps measuring 40/30 x 10 x 10 cm, baited with slices of carrot (10-20 g) and with some dry hay added. The traps were positioned at holes and in runways and successively moved through the study area during a trapping session [20]. To minimize the potential risk of environmental exposure, trapping was not conducted in very hot weather or during periods of heavy rainfall.

Within one trapping session I tended to avoid repeated handling of juveniles and, when recaptured and the ear tag could be seen when in the trap, they were generally released without further investigation. Recaptured juveniles were examined when the ear tag could not be seen in the trap, when captured just after the traps had been moved or when captured in a different trapping session. Likewise, many adults recaptured within a few days after their first capture were released without handling. To enable this, most adults were marked on the tail with white wax crayon intended for use on farm animals, a mark that lasted only a day or two. Their release without measuring was to avoid handling animals repeatedly and because repeated measurements within a few days were of little interest. When starting a new trapping session, all ear tags were read. Some water voles became "trap-happy", repeatedly entering the same or a nearby trap and, especially the larger juveniles, eating the bait. Eating several slices of carrot in a short time could cause an immediate increase in weight resulting in a seemingly high growth rate, termed the bait effect. Voles were weighed in a cotton bag using Pesola spring scales (300 or 500 g). They were marked in one ear with individual numbered ear tags (National Band and Tag Company #1005-1 Monel). Most voles were marked and released within 30 minutes after entering a trap and very few remained in a trap for more than two hours [20]. Lost tags were not accounted for.

Three age classes were recognized: juveniles in their first summer, overwintered subadults in spring and overwintered sexually mature adults. The distinction between the two last groups was blurred, as the subadults grew into adults. This morphological change occurred in April and May, so only overwintered voles that weighed less or equal to 150 g in these two months were classified as subadults. Juveniles were distinguished from overwintered voles by their smaller size and shorter fur. They had a short fur mostly in pristine condition, growing longer as they grew in size and towards the end of the summer. Winter fur was long, dense and clearly seen in overwintered animals. Voles were grouped into 20 g interval weight classes, starting from 21 g (i.e., 21-40 g, 41-60 g, etc.), to avoid a potential bias resulting from differences in sample sizes. The difference in weight between one capture and the next divided by the number of days between captures, gave a growth rate in g/day. I assumed a birth weight of 5 g. Generally, no sexual difference in weight was found in this population [20].

As subadults grew into adults they kept their long, shaggy (and eventually worn and torn) winter coat throughout the summer and did not moult into a specific summer coat. However, following the end of reproduction in late summer, a very few adults in good condition did start the moult into a new winter coat. At this time, other adults had lost a significant amount of their weight. Consequently, after August large juveniles with developing winter fur could potentially be mistaken for an adult with a full new coat. This potential error was, however, negligible, both because, in the early August trapping session, few juveniles had attained adult size and grown a full winter coat and because very few adults survived the summer and fully moulted into a pristine new coat.

All analyses were undertaken using the statistical software SPSS ver. 28. The basic data are given in Additional file 1. Results are presented as mean ± 1 SD. Statistical methods include chi-square (χ^2), analysis of variance (F), Pearson's correlation (r) and regression (r). Linear growth curves for a few juveniles in captivity was given by [20], and a few other publications included data on growth [19, 25-28]. These were used to make linear regressions for juvenile growth, for comparisons with my data. In my study, age was strictly speaking unknown, so only a few tentative suggestions about the relationship between age and size are made.

3. Results

3.1. Growth Rates and Winter Survival in Juveniles

The two smallest juveniles trapped weighed 21 g and were assumed to be 12-15 days old, and only 24 juveniles weighed less than 29 g. The first young were captured in the middle of May (Figure 1) and would have been born in the first days of May. Sixteen data points from Figure 1 in [20] (captive animals), from 1-55 days old and 6-110 g, gave a linear regression (1): age=1.31+0.45*weight (r^2=0.99). Using 11 less homogeneous data points from other references (see Method) gave a similar equation (2): age=0.77+0.46*weight (r^2=0.87).

Accordingly, a 60 g juvenile would be 28.3 (1) and 28.4 (2) days old, respectively. At 100 g it would be 46.3 (1) and 46.8 (2) days old, respectively. These estimates fitted my data (Figure 1) relatively well, but the growth was not strictly linear but logistic, contrary to the data referred to above. When using a "starting point" of 21 g at 14 days old, the near upper part of the data points in Figure 1 indicated that by the middle of June, i.e., 40-50 days old, the corresponding weight was 100-120 g and that a 160 g juvenile could be around 90 days old. The earliest born juveniles approached an asymptote at around 150-160 g in late July, perhaps even in early July for some very early born juveniles (Figure 1). These are in the upper end of the growth rates, most juveniles weighed far less even at the end of the summer. Very few juveniles reached more than 170 g and none were lactating (the easiest sign of reproduction). In the late season (from late July) mean weight of juveniles was 111.1±30.1 g (n=1340) and when including only juveniles above 100 g their mean weight was 126.8±16.9 g (n=938). Mean weight in October, i.e., after the summer growth, was 144.6±17.7 g (n=35). In comparison, mean weight of 17 overwintered males in April was 178.8±53.7 g and of 8 females 152.2±23.9 g. In a small sample from another island 118 km further north, mean weight was only 118.6±15.3 g in November (n=16).

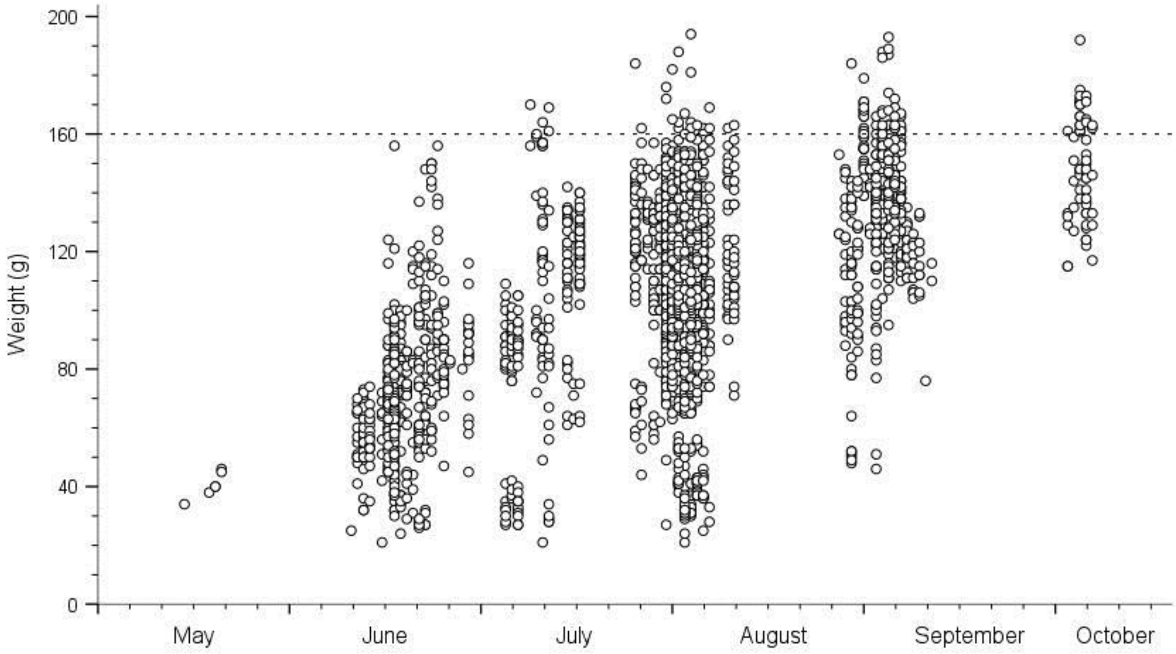

Figure 1. *Weight of juvenile water voles across the season, including recaptures. Overall trapping effort differed between months.*

Considering weights below 60 g, most young appeared to be born in May and June, some in July and none in August or later (Figure 1). The first few litters may have been born in the last days of April. The smallest juvenile recaptured the following year weighed 44 g in its first year (in August). The growth rate declined significantly with increasing weight (r=-0.78, p<0.001, Figure 2, Table 1). It varied greatly between weight classes (Table 1), from being highest initially to negative in the two largest classes. The very large standard deviations indicated large variation in growth rates within each class, being largest in classes 7-8 (Table 1). Using the linear regression (1), the 20 g weight classes in Table 1 roughly corresponded to 8-days intervals (the last corresponded to 6 days), starting at 11 and ending at 89 days old.

In juveniles, some of the large variation in growth rates, from around -20 to + 20 g/day (Figure 2), could be due to a bait effect. When recaptures within one day of the first capture were excluded, nearly all growth rates lay within between +/- 5 g/day, with only two > 5 g and three < -5 g. No difference in growth rates between the three years 2006-2008 was found (F=0.42, d.f.=2, 311, p>0.05).

Table 1. *Mean ±1 SD growth rate (g/day) within-year and across weight classes, with percentages caught (a-d). Growth rates are given for juveniles and overwintered voles (subadult and adults). Percentages caught for juveniles: a) among all caught (first capture only) in their first summer, b) among those recaptured in their first summer, and c) among those that survived the winter and was recaptured the next year. d) Percentages caught for subadults and adults: among all caught. N=overall sample size.*

		Juveniles				Subadults & adults	
Weight class (g)		**Growth rate**	**a) All caught**	**b) Re-captured**	**c) Over-wintered**	**Growth rate**	**d) All caught**
1	21-40	2.46±0.63	5.6	3.0	0		
2	41-60	2.83±4.01	7.3	6.3	6.4		
3	61-80	1.48±1.70	13.8	12.6	5.0		
4	81-100	1.06±2.38	18.7	13.2	10.6		0.1
5	101-120	0.58±3.83	22.4	20.4	24.1	1.78±6.84	3.0
6	121-140	0.26±3.07	21.6	26.1	28.4	1.45±6.00	7.2
7	141-160	-0.25±5.47	8.8	13.2	22.0	0.37±6.74	11.8

		Juveniles				Subadults & adults	
Weight class (g)		Growth rate	a) All caught	b) Re-captured	c) Over-wintered	Growth rate	d) All caught
8	161-180	-2.25±6.66	1.4	5.1	3.5	1.14±4.75	18.3
9	181-200	-	0.4	0	0	-0.31±6.24	28.7
10	202-220					-2.09±8.36	18.1
11	>221					-2.69±7.36	12.7
N		333	1870	333	141	277	1047

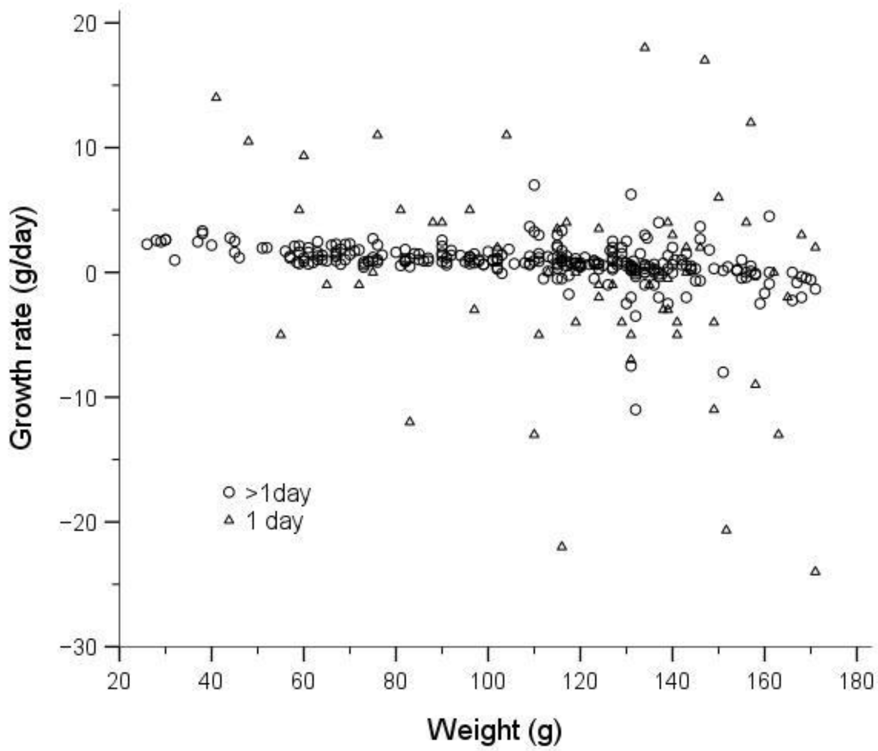

Figure 2. *Growth rates of juvenile water voles plotted against body weight, with those recaptured the next day indicated by triangles.*

Average juvenile weight from all data but including only first capture (one measurement per animal) was 101.3 g, whilst juveniles that survived their first winter averaged 118.6 g in their first summer, indicating slightly better survival among heavier juveniles (F=9.0, d.f.=1, 416, p<0.01). When the proportions of juveniles in the various weight classes were compared (Table 1), 53% of all juveniles weighed fell within the classes 5-7, compared to 59% of those recaptured their first summer and 75% of those that survived their first winter. The number of overwintered voles in weight classes 2-8 differed significantly from the number in these classes among all captured juveniles (χ_2=42.8, d.f.=7, p<0.001). Relatively more overwintered voles fell in the classes 6-7 and fewer in the classes 3-4 (Table 1).

An overall approximate survival rate was estimated for the main study site Trolløya (2005-2018) as the number of overwintered voles one year divided by the number of juveniles the previous year: 0.37±0.23 (n=13 years), minimum 0.15 and maximum 0.89. (This rate does not account for lost tags or the fact that the population was not entirely closed.)

3.2. Growth and Survival in Subadults and Adults

Among voles that were measured in two different years, the weight in their first year was significantly correlated with the weight in their second year, although the correlation coefficient was relatively small (r=0.23, p<0.01, n=147). A typical example was female no. 450: 16 June 2006 = 80 g, 16 July 2006 = 130 g, 4 September 2006 = 156 g, 6 June 2007 = 213 g and 29 June 2007 = 229 g. The lightest adult caught in the late season weighed only 128 g (a female in early September), six adults weighed 141-160 g and all others more than 160 g. Among adults initially weighing more than 160 g and recaptured later in the summer, weights at first and second capture were identical (198.0±22.1 vs. 197.8±20.3 g, n=212). Only six water voles were known to survive their second winter, weighing 199.3±29.7 g in their last summer, but by this time many ear tags would have been lost. The mean for adults captured in June and later was 191.4±22.5 g (n=74) for males and 201.2±24.1 g (n=203) for females.

Growth rates in the lighter weight classes (mostly subadults) were positive and initially high (Table 1), only to diminish with increasing weight and become negative in the three heaviest classes. Adult growth rates during the summer varied between +21 and -35 g/day, the extremes possibly being explained by the bait effect. When recaptures within the first two days were excluded (adults moved more than juveniles), only four growth rates fell below -5 g and five above +5 g.

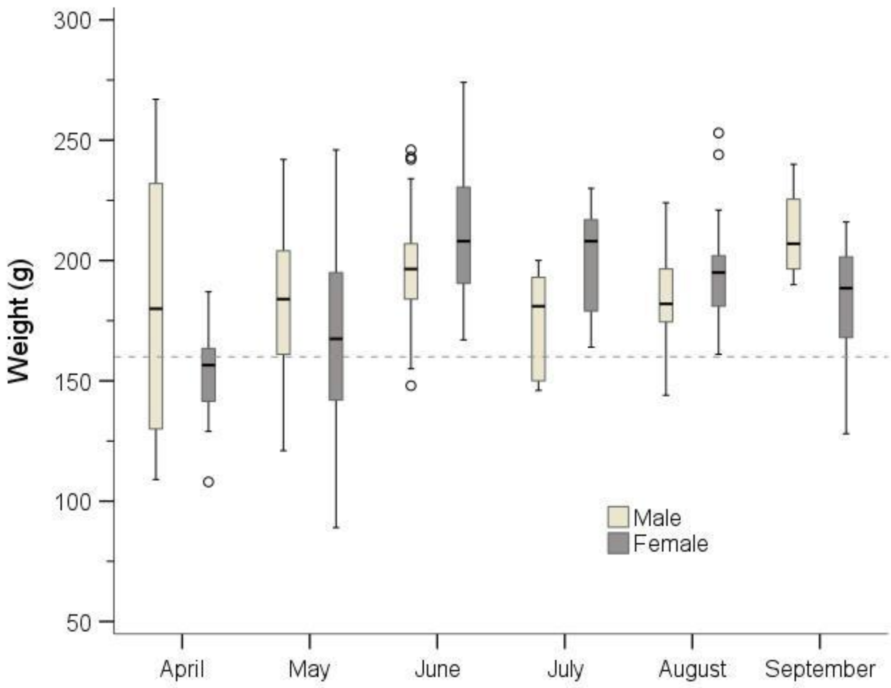

Figure 3. *Boxplot of the weight of subadult and adult water voles by sex and month. The dashed line represents 160 g.*

One overwintered female weighed as little as 89 g, all other subadults weighed more than 100 g. Some grew to adult size already in April (voles were trapped only one April), when 16% weighed less than 121 g, 36% between 121 and 160 g and 48% more than 161 g (n=25). In May, only 4.8% weighed less than 121 g, 30.8% weighed 121-160 g and 64.3% weighed more than 161 g (n=581). A huge variation in male weight was found in April, whereas female weight varied most in May (Figure 3, in this boxplot the horizontal line is the median, 50% of the values fall within the box, the "arms" represent the smallest and highest value that are not an outlier, and the circles represent outliers). Most (82.4%) adults were caught early in the season and only 17.6% in the late season (n=716). Despite a similar trapping effort, 57.3% of adult captures were in May and only 14.7% in August. In comparison (of trapping effort), only 0.1% of the juveniles were caught in May and 57.1% in August. Among males, 12.8% were caught late in the season compared to 20.3% among females. The proportion of males to females caught was 0.59 in the early season and 0.34 in the late season (χ_2=6.22, d.f.=1, p<0.05, n=714).

On average, overwintered animals weighed only 8.1 g less in the early vs. late season, but the variance was three times greater in the early season (1203.4 vs. 396.4, compare with Figure 3). When only adults weighing minimum 150 g were included, thereby excluding subadults in the early season and four "underweight" adults in the late season, there was no difference between the early vs. late season weights (F=1.06, d.f.=1, 889, p>0.05).

4. Discussion

No specific "optimal" weight or weight range for survival for water voles was found in this study. I expected to find the optimal range for juveniles in weight class 7 (141-160 g), but even in late summer most voles weighed less than this. However, juveniles weighing more than 100 g survived better, otherwise weight simply did not seem crucial to survival. The "optimal" range may have been between 100 and 160 g, but this is too broad to indicate a specific "ideal" weight for survival. From around 100 g, the growth rate declined steadily as an asymptote was approached. There was no indication that small juveniles in late summer had a higher growth rate in order to face the winter. Even young born early in the summer did not always reach 150 g. Heavy predation on the first-born litters most likely partly explained why so few large juveniles were found in late summer. In conclusion, none of the hypotheses were well supported. The expected asymptotic weight was not clearly defined, and body weight did not have a significant influence on survival in this population of water voles.

Most adults even in late summer weighed more than 160 g and did not reduce their weight to a reduced "optimal" range in preparation for surviving the next winter, i.e., well after reproduction had ended but before the vegetation had entirely stopped growing. Some adults did indeed lose weight during the summer, but this appeared to be related to other factors, foremost to the investment in reproduction (and associated social stress). Adult size is not a prerequisite to sexual maturity, because both subadult males and females may start to reproduce [25, 29]. Large size in adult females can be related to litter size [30], while in adult males it is likely to be associated with dominance and increased mating success [6, 14]. This would explain why male subadult water voles start the growth to adult size earlier than females [20]. In subadult females, the growth to adult size may accompany their first pregnancy.

Information about growth and reproduction in water voles in the literature is fragmented. Some authors have classified water voles as either juveniles or adults based on weight alone, with the separation set at 140 g [31] or 175 g [32] and used the growth curve in [25] (captive animals) to estimate age. Generally, in the northern part of the species' distribution, the first matings (conceptions) occur in April, gestation takes 20-23 days (average 21.6, [26, 28], and weaning starts at 11-13 days [32, 33] or 15 days [26]. Birth weights range from 3.3-7.8 g, averaging 6.22 g for males and 6.01 g for females [26]. In captivity, juveniles reached the asymptotic weight at 10 weeks [32]. Young may "leave the nest weighing as little as 30 g" [20] or 10 days old [26], perhaps permanently when 14 days old [27].

In a free-living population in the southern part of the species' range (Spain), breeding was recorded between March and October [30, 34]. Most pregnant females were older than 70 days and reached sexual maturity weighing 76-96 g while males became sexually mature weighing 65-95 g [30, 34]. Young in the laboratory became sexually mature at 40-90 g, the youngest sexually active male was 43-47 days old, the youngest female 67 days [26]. Another author [27] stated: "…some females reached sexual maturity when they were only 38 days old (77 g), with a median age of 60 days (110 g) at maturity when they were born before July. As all the young born before July mature in their year of birth it is surprising that in Britain, so few reproduce in the same season. In Norfolk only 10% of the young females of the year lactated….". Threshold weights of 115 g for males and 112 g for females at which juvenile water voles reached breeding condition were estimated by [35]. Presumably, only water voles born early (before July) will reproduce in their first summer and "most reach sexual maturity after their first winter" [19]. This author also stated that water voles "probably need to attain a weight of 170 g in order to survive the winter". At the end of the breeding season, adult water voles may reduce their size, possibly to enhance winter survival [28]. These authors stated: "In contrast to other vole species, *Arvicola terrestris* L. demonstrates increased body weight after parturition relative to that at mating. After weaning the mother's body weight considerably decreases…." Another study [36] concluded that juvenile females breeding in their first year had higher mortality during the winter.

Some of the above facts are difficult to reconcile with my data. In mammals, fetal growth rates generally accelerate with time, this accelerating growth ends near birth and is replaced with a phase of decelerating growth until adult mass is achieved [1, 2]. Voles differ from this trend, having both a fetal, a juvenile and a subadult growth phase. They may reach sexual maturity at a very young age and small size, presumably followed by additional growth to adult size (a better-documented case is the Norway lemming *Lemmus lemmus*, another relatively large species [37, 38]). In a study of juvenile growth, sexual maturation would be "noise" confounding the data [12]. I found a wide individual variation in growth rates as well as in pre-winter size, and to reach 100 g (about half the adult size) took around 40 days. Such a large variation in growth rates has also been found in the field vole *Microtus agrestis*, whose juveniles took around 20 days to reach the asymptotic weight of 21 g, about half the adult size [12].

Water voles and field voles have about the same gestation length, litter size and number of litters per season. Consequently, the water vole has no reproductive advantage compared to other voles and its large size does not give better protection against predators. It may have an advantage in direct competition for living space with *Microtus* species, but this advantage should not require that much larger size. Thus, the benefits of much larger size in this burrowing vole are not obvious, unless it is an adaptation to swimming in cool waters. A cost of large size could be that many or most juveniles do not breed in their first summer, with stark implications for population growth rates.

In my study population in northern Norway, no voles breeding in their first summer could be confirmed, and, most notably, no lactating first-summer female was ever found. I did not register vaginal plugs and it remains possible or even likely that some juvenile females had mated, but without litters being produced. Consequently, many would be dead by the next spring when reproduction could start. The young are thought to leave their nest and become trappable at 14 days of age [19, 25]. This is, surprisingly, identical to the much smaller *Microtus* species. However, I suspect that the smallest young measuring 21-30 g were in fact not fully weaned and thus had not fully abandoned their nest, an event that more likely happened at 30-40 g, i.e., around 20 days of age. This could be explained by differences between free-living and laboratory-bred water voles or by differences between populations.

The water vole is the largest among all vole species, with a maximum male weight recorded in my study site of 267 g. The difference in size between juveniles/subadults and adults is striking, following rapid growth in spring. In my population, mortality due to predation was very high [20], consequently, breeding early (as first-summer juveniles) could have been advantageous pending the predation risk. This would have increased the population size much more than what was actually found [20]. Adults had a high mortality rate in the summer, presumably because they spent more time foraging and were more active outside burrows thus increasing predation risk [20, 25]. Voles reproducing in their first summer would have been exposed both to a similar predation pressure as well as to a lower survival rate during the winter (i.e., if the toll of reproduction lowers survival). They would have had to compete with the more dominant adults and their offspring might have a lower survival rate, as they would be likely to breed at the highest population density of the year. Social stress or inhibition by adults to become sexually mature may possibly also lead to postponed reproduction [35]. This is a density-dependent factor, but such factors are not always of significance [8, 12]. By postponing reproduction until next spring, the juvenile water voles in my study site avoided most of these variables and could start reproduction with less competition and a fresh vegetation growth. A vole cannot calculate the risk of predation during the winter, a risk that may be individually reduced by staying more below ground.

5. Conclusions

No specific "optimal" weight or weight range to survive the winter was found in this population of water voles. Juveniles in the autumn weighing between 100 and 160 g, as most did, seemed to have equal survival chance. This range is too broad to define an optimal weight. Juveniles smaller than this may, however, have poorer survival rate in the winter. Larger juveniles had only slightly better survival than smaller. Adults did not appear to reduce their weight in the autumn, but few survived the summer and almost none the next winter. Overwintered subadults in spring weighed about the same as juveniles did in the autumn. Juvenile growth rates varied much, and juveniles did not reach a clear asymptotic weight, but its maximum was around 150-160 g, as very few reproduced in their first summer. A flexible and adaptable strategy in both growth and winter weight were more likely than any fixed strategy and optimal weight for survival. Due to a high predation rate and risk, survival depended less on size and more on chance and agility. These results are significant to understand the species' population dynamics and the potential for population outbreaks, and of relevance to the understanding of population dynamics and demography in microtine rodents.

Supplementary Material

The supplementary material can be accessed at https://doi.org/10.11648/j.ajbio.20241203.11

Acknowledgments

Trapping and tagging water voles were approved by the Norwegian Environment Agency. Thanks to Rob Barrett for improving the style and spelling and for many welcome suggestions to the manuscript. Frode Johansen ensured safe boat transportation to the study sites.

Ethics Approval

This project was approved and licensed by the Norwegian Environment Agency, no further approval or evaluations were required. Trapping was performed in accordance with Norwegian guidelines and regulations. No animal was harmed or died during trapping or handling.

Author Contributions

Karl Frafjord is the sole author. The author read and approved the final manuscript.

Consent for Publication

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Conflicts of Interest

The author declares no conflicts of interest.

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