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Does food supply affect egg size in Dunlin *Calidris alpina schinzii*?

Påverkar födotillgången äggstorleken hos kärrsnäppa Calidris alpina schinzii*?*

LARS-ÅKE FLODIN & HENRY HIRSIMÄKI

Abstract

Food supply in relation to egg volume was studied in Dunlins Calidris alpina schinzii in the Getterön area, southwest Sweden 1995–1997. Food supply generally decreased from 1995 to 1996, and tended to increase from 1996 to 1997. Within a year, food supply generally increased over the breeding season. Mean egg volume followed the food supply pattern, i.e. egg volume decreased between 1995 and 1996, and increased between 1996 and 1997. However, within a year there was no change in egg volume over the season despite an increased food supply. The latter result may be a consequence of later breeding females investing less in their clutches, or that a seasonal increase in food supply compensated a lower potential for egg volume in late females (that may be of lower quality).

Lars-Åke Flodin, Rannevägen 12, 432 95 Varberg, Sweden (e-mail: larsakeflodin@telia.com).
Henry Hirsimäki, Nyhemsgatan 6 B, 432 35 Varberg.

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Introduction

For many animals there is a positive relationship between egg size and the growth or survival of offspring (Williams 1994, Christians 2002 and references therein). There was a positive relationship between egg size and hatchling size or growth of the offspring in about 50% of the studies reviewed by Williams (1994), and this relationship seems to be more pronounced among precocial than altricial species.

The relationships may, however, have several explanations and attempts have been made to separate effects of large eggs on the survival and growth of offspring from effects that are due to parental quality. Such effects might depend on e.g. antipredator behaviour, quality of the territory (nutrient for egg formation and food for the offspring) or the parents' ability to incubate the eggs and protect the offspring. By exchanging eggs between nests with small and large eggs, it has been found that the ability to produce large eggs is often correlated with chick-rearing ability (see Blomqvist et al. 1997 and references therein). The ability to produce large eggs depends on a variety of factors. In many wader species, egg size is correlated with the size of the female (Väisänen et al. 1972, Jönsson 1987, Blomqvist & Johansson 1995). The age of the female may also be of importance. Older and more experienced females produce larger eggs in Semipalmated Sandpiper *Calidris pusilla* (Gratto et al. 1983) and Redshank *Tringa totanus* (Thompson & Hale 1991). In Oystercatcher *Haematopus ostralegus* and Greenshank *T. nebularia,* however, older birds produced smaller (Jager et al. 2000) and lighter (Thompson et al. 1986) eggs.

The positive effects of hatching from a large egg may be short-term. Chicks of waders and gulls from large eggs survived better than those from small ones during their first week (Parsons 1970, Galbraith 1988a, Grant 1991, Blomqvist et al. 1997). Chicks from large eggs have benefits during their first days particularly if weather conditions make foraging difficult. This is a critical period for most wader chicks since their thermoregulatory capabilities are poorly developed (Norton 1973, Chappel 1980).

The availability of food affects egg size in Lapwing *Vanellus vanellus.* Females that forage in nutrient-richer areas produce larger eggs (Galbraith 1988b, Blomqvist & Johansson 1995). However, the relationship between egg size and good supply of food is not always clear. When the food supply is very rich, other factors have a relatively greater effect on individual differences in egg size (Grønstøl 1997).

Erckmann (1983) showed that the weight of female waders did not differ significantly before and after egglaying. This made him conclude that female waders do not deplete nutrient reserves appreciably during laying, and apparently acquire nutrients for egg formation primarily during the laying period. The hypothesis that arctic waders are dependent on the food supply at the breeding ground for egg formation, was confirmed in a study by Klaassen et al. (2001). Changes in food supply will affect egg volume in species like the Dunlin *Calidris alpina schinzii*, in which females arrive at the breeding grounds about two weeks before they start egg laying (Jönsson 1988).

In this study, we analyse the relationship between food supply and egg size in Dunlins breeding on cattle-grazed coastal meadows in southwest Sweden. We specifically want to test two predictions, which should apply if the food supply is crucial for egg formation: (1) There should be a covariation in between-year trends in egg size and food supply, and (2) there should be a covariation in egg size and food supply over the breeding season within a year.

Study area and methods

The study was carried out from the end of March to the end of June 1995–1997 at Getterön, a nature reserve on the west coast of Sweden. Getterön is about 355 ha in size (water - 103 ha, reed and sedge *Phragmites australis, Scirpus maritimus* and *S. tabernaemontani* - 30 ha, grassland *Festuca rubra-Juncus gerardi* and *Deschampsia cespitosa* - 185 ha, arable fields - 26 ha, and other land - 10 ha). The Himleån River mouth is located within the reserve.

For the past several years, a study of the Dunlin has been in progress on the west coast of Sweden, and most Dunlins are therefore marked with individually unique combinations of colour rings (Blomqvist & Johansson 1991). We identified the colour ringed birds when they arrived in the spring, located their nests, and caught and colour-ringed previously unringed adults and chicks. Since 1978 breeding Dunlins have been censused annually (Flodin & Hirsimäki unpubl.).

Most Dunlin nests were situated in the 20 ha of grassland in the northeast section of the reserve (Figure 1). The vegetation in this area, predominated by *Deschampsia caespitosa* with *Agrostis stolonifera* and *Elocharis uniglumis* in lower and wetter parts, is mostly well grazed, but there were some minor sections with tussocks and higher grass where the Dunlins nested.

Figure 1. Map over the study area.
Karta över undersökningsområdet.

In spring, the Dunlins forage exclusively in three places on and close to the reserve (Figure 1). (1) Along the shore of a man-made pond (*the Pond*). The level of the water is stable and not affected by sea water fluctuations. The salinity is regulated and is usually just below 1%. (2) South of the road to Getterön (outside the reserve), *the Southern bay* has fine bottom sediments with some gravel. The water has almost the same salinity as the sea, i.e. just above 2%. (3) In the outer part of Farehamnsviken (*the Bay*). The water is usually rather fresh due to the mouth of the River Himleån. When the weather is stormy, seawater is pressed into the bay, resulting in higher salinity. The bottom is made up of very fine sediments.

From the beginning of March and until the first days in May, the reserve was visited almost daily. The number of Dunlins was registered and individuals identified by their colour rings. To be sure of the identity, it was in some cases necessary to catch an adult bird on its nest. The time eggs had been incubated was estimated from their floating characteristics (van Paassen et al. 1984, Blomqvist 1996). Egg size was measured with a vernier caliper to the nearest 0.1 mm and the volume was calculated as $V = 0.40938 \times \text{length} \times \text{breadth}^2 + 1.092$ (Väisänen

1977). Throughout this study, "egg volume" is based on the mean egg volume of a clutch.

To determine the food supply available for foraging Dunlins, we studied the bottom fauna of invertebrates on the three sites where Dunlins used to forage (see above). Samples were also taken from a small lagoon close to the breeding area. In 1995, samples were taken three times; mid April, mid May and early June. In the Bay, sampling was extended to seven times. In 1996 and 1997, the bottom fauna was sampled only once in the middle of April (just before the start of egg-laying).

A system of co-ordinates was placed on the map of the foraging sites, and on each occasion the co-ordinates for sampling were chosen at random. When sampling for the seasonal variation in food supply in 1995, 15 samples were taken each time. For comparison between years, the sample size was doubled to 30 samples (1996 and 1997) at each of the four sites. The samples were taken with a core sampler of plastic (diameter of 10 cm) which was pushed down 5 cm into the bottom sediment. The core was washed and the animals were sorted, counted and identified, in most cases to genus or a higher order.

The biomass, measured as ash free dry weight (AFDW), was estimated by drying the animals in an incubator at 105º C for a period of 24 hours and then weighed with an accuracy of 10^{-4} g. Then the animals were burned in an oven at 550º C for three hours and weighed with the same accuracy. The ash free dry weight is the difference between the two weighings. In the analyses, only animals that have been reported as prey items for Dunlins were included (Norlin 1965, Bengtsson & Svensson 1968, Glutz von Blotzheim et al. 1975, Cramp & Simmons 1983). Large individuals (> 1 cm) of bivalves and gastropod snails, together with the lugworms *Arenicola marina*, which live so deep in the sediment that they are out of reach for Dunlins, were excluded.

All statistical tests are two-tailed. In cases where a female laid egg in more than one year, one of the years was chosen at random to avoid pseudoreplication.

Results

During 25 days in April 1997, we made 171 observations of foraging Dunlins. These observations showed that when the water level was low Dunlins preferred to forage in the Bay, however, when the water level was high they instead fed in the Pond. The flock of Dunlins regularly disappeared out on the islands west of Getterön. When it was possible to observe their behaviour, they were resting on small stones in the water close to the islands (M. Nord personal communication). Observations of Dunlins were rarely made on other sites and their behaviour was identical over the three years.

Density of potential prey

The biomass and numbers of potential prey at the different feeding sites are shown in Table 1. On bottoms with fine sediments in the Bay, the invertebrate macrofauna was dominated in numbers by the amphipod crustacean *Corophium volutator* (67%), the polychaete worm *Hediste diversicolor*

Table 1. Mean prey numbers (number of animals/m^2 ±SE) and mean prey biomass AFDW g/ m^2 ±SE) in the second half of April 1995–1997 (average of 15 subsamples in 1995 and 30 in 1996–1997). AFDW = ash free dry weight.
Medelantal bytesdjur och bytesdjurens medelbiomassa på olika lokaler under andra halvan av april 1995–1997 (medelvärden för 15 provtagningar under 1995 respektive 30 under 1996–1997). AFDW = den askfria torrvikten.

	1995		*1996*		*1997*	
Locality *Lokal*	Prey numbers *Antal byten*	Prey biomass *Bytesbiomassa*	Prey numbers *Antal byten*	Prey biomass *Bytesbiomassa*	Prey numbers *Antal byten*	Prey biomass *Bytesbiomassa*
The Bay	5520±281	3.47±0.93	1900±186	1.36±0.18	2027±142	1.09±0.12
Southern bay	3623±428	2.44±0.66	3729±390	0.96±0.15	3890±287	1.31±0.17
The Pond	1312±148	3.18±0.70	305±63	0.05±0.01	339±85	0.04±0.01
Northeast corner	296±64	0.11±0.02	89±20	0.05±0.01	762±112	0.12±0.02

(15%) and *Oligochaeta* (17%). The first two also dominated in terms of biomass (>99%). There were also a few individuals of non-biting midges (Chironomidae larvae) and the polychaete worm *Pygospio elegans*. We recorded differences between the three years in both numbers (Kruskal-Wallis ANOVA, H=33.66, n=75, df=2, p<0.001) and biomass (H=29.79, n =75, df=2, p<0.001). In both cases, there were significant differences between 1995 and the two following years (Tukey-test, p<0.001), but the differences were not significant between 1996 and 1997 (Tukey-test, p>0.05).

The macrofauna in the Pond was dominated by the polychaete worm *Hediste diversicolor* (59%). Larvae of non-biting midges *Chironomidae* (13%) and biting midges Ceratopogonidae (24%) were also numerous. The difference was significant for prey numbers (H=26.84, n=75, df=2, p<0.001) and biomass (H=36.70, n=75, df=2, p<0.001). The differences between 1995 and the following years were significant for both prey numbers and biomass (Tukey-test, p<0.001). Between 1996 and 1997, the differences were not significant (p>0.05).

In the lagoon close to the breeding area of the Dunlins (the *Northeast corner*), non-biting midges *Chironomidae* (86%) were the most common potential prey. Aquatic bugs (Corixidae), Oligochaeta, biting midges Ceratopogonidae, water beetles *Haliplus sp.* and mites Hydrachnidae were found in low numbers. Even in this area, there were significant differences between years in prey numbers (H=35.76 n=75, df=2, p<0.001) and biomass (H=27.44, n=75, df=2, p=0.001). As in the Bay and the Pond, the decline between 1995 and 1996 was significant for both prey numbers (Tukey-test p<0.001) and biomass (p<0.01). Between 1996 and 1997, the increase was significant with regard to prey numbers (p<0.001) and biomass (p<0.001). Compared to the other feeding areas, prey biomass was much lower in the Northeast corner (Table 1).

In the Southern bay, the macrofauna was more varied. The most numerous taxa were the polychaete worm *Pygospio elegans* (27%), mudsnails *Hydrobia sp.* (27%) and Oligochaeta (33%). The polychaete *Hediste diversicolor* had large impact on the biomass. Other potential prey species were small individuals of *Littorina sp.,* the bivalves *Macoma baltica, Mya arenaria,* and *Cardium edule.* The crustacean *Gammarus sp.* and *Coriophium* and the polychaete worms *Eteone longa* and *Scoloplos armiger* occurred in low numbers.

Contrary to the other foraging areas, there were no significant differences in prey numbers between years (H=3.24, n=75, df=2, p=0.197). For prey biomass, the differences were significant (H=23.52, n=75, df=2, p<0.001), with a marked decrease between 1995 and 1996 (Tukey-test, p=0.001), but not between 1996 and 1997 (p>0.05).

To summarise, there was significantly more prey biomass in 1995 than 1996 at all four foraging areas, and for prey numbers the same was true in three of the four areas. The increase between 1996 and 1997 was only significant in the Northeast corner.

Variation in food supply over the breeding season

There was no covariation in food supply at the four foraging areas over the season (Table 2). At the Bay

Table 2. Mean prey numbers (number of animals/m^2 ±SE) and mean prey biomass AFDW g/ m^2 ±SE) in mid April to early June 1995 (n=15 at each site and sampling occasion). AFDW = ash free dry weight.
Medelantal bytesdjur och bytesdjurens medelbiomassa på olika lokaler från mitten av april till början av juni 1995 (n=15 på varje lokal vid varje provtagningstillfälle). AFDW = den askfria torrvikten.

	Mid April		Mid May		Early June	
Locality *Lokal*	Prey numbers *Antal byten*	Prey biomass *Bytesbiomassa*	Prey numbers *Antal byten*	Prey biomass *Bytesbiomassa*	Prey numbers *Antal byten*	Prey biomass *Bytesbiomassa*
Southern bay	3623±428	2.44±0.66	7522±1021	3.88±0.57	8390±359	4.01±0.28
The Pond	1312±148	3.18±0.70	432±57	1.04±0.71	812±97	1.15±0.19
Northeast corner	296±64	0.11±0.02	135±42	0.04±0.02	5435±2384	1.00±0.26

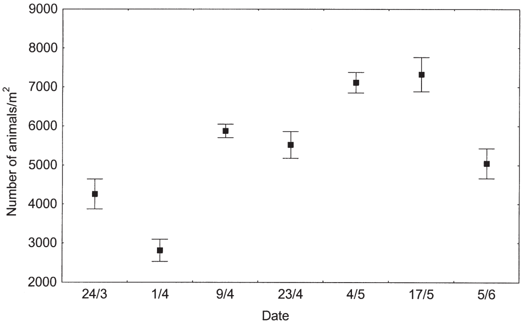

Figure 2. Mean prey numbers (number of animals/m^2 ±SE) at the Bay 1995 (n=15 at each site and sampling occasion).
Medelantal bytesdjur i Viken 1995 (n=15 på varje lokal vid varje provtagningstillfälle). AFDW = den askfria torrvikten.

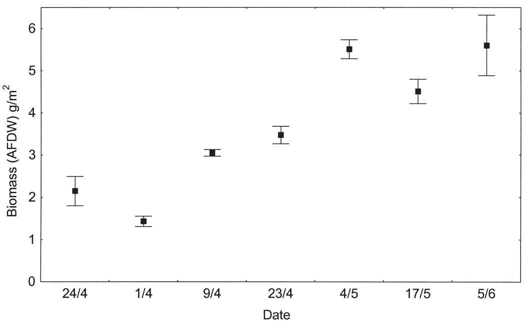

Figure 3. Mean prey biomass (AFDW g/m^2 ±SE) at Viken in 1995 (n=15 at each site and sampling occasion).
Biomassan i Viken 1995, mätt som den askfri torrvikt (n=15 på varje lokal vid varje provtagningstillfälle).

with brackish water the macrofauna was sampled on seven different occasions between March 24 and June 5, 1995. Prey numbers tended to increase (Spearman r_s=0.54, n=7, p=0.22; Figure 2) and prey biomass increased significantly (Spearman r_s=0.93, n=7, p<0.01; Figure 3) over this period.

In the Southern bay, with marine conditions, there were significant differences in prey numbers between the three sampling occasions (Kruskal-Wallis ANOVA, H=18.63, n=45, df=2, p>0.001). Between April and May there was a significant increase in prey numbers (Tukey-test p<0.01), but not between May and June. The pattern for prey biomass was similar (H=12.54, n=45, df=2, p=0.002), with a significant increase between April and May (Tukey-test p<0.01) but not between May and June (p>0.05).

In the brackish water of the Pond, there were significant changes in both numbers and biomass (H=19.87, n=45, df=2, p<0.001 and H=15.11, n=45, df=2, p=0.005, respectively). For both prey numbers and biomass there was a significant decrease from April to May (Tukey-test p<0.001 in both cases), and then a non-significant increase from May to June.

In the Northeast corner there was significant variation both in prey numbers (H=14.93 n=45, df=2, p<0.001) and prey biomass (H=30.26, n=45, df=2, p<0.001). However, the decrease between April and May was not significant (Tukey-test p>0.05), whereas the increase between May and June was significant both for prey numbers and biomass (p>0.001 in both cases).

To summarise, prey numbers, and particularly their biomass, increased continuosly during the breeding season in the more marine foraging areas (the South bay and the Bay). In The Pond and the Northeastern corner, with brackish water, the numbers tended to decrease from April to May and increase significantly thereafter.

Table 3. The annual mean egg volume (cm^3±SE) in Dunlins 1995–1997.
Medeläggvolymen hos kärrsnäppa 1995–1997.

Year *År*	Egg volume *Äggvolym*	Number of clutches *Antal kullar*
1995	9.26±0.072	9
1996	8.79±0.079	8
1997	9.23±0.087	8

Egg volume patterns

The egg volume differed between the three years (Kruskall Wallis H=11.96, n=25 clutches, df=2, p=0.025). The egg volume decreased between 1995–1996 (Tukey-test p<0.001; Table 3) and it increased between 1996–1997 (Tukey-test p<0.05; Table 3). However, there was no difference between 1995 and 1997. Of four pairs whose eggs were measured both in 1995 and 1996, three had smaller and one greater egg volume in 1996.

Clutches were measured during the period 26 April to 27 May, and there was no trend for a seasonal change in egg volume over this period (Spearman

r_s=0.14, p=0.62, n=13 clutches). The lack of a decrease in egg volume over the season may be explained by the increased food supply during this period (see above).

Discussion

The winter temperature and duration of periods with low water influence the species composition and population densities of the invertebrate fauna on the Swedish westcoast (Karlsson et al. 2000). The observed difference in food supply between years (see Table 1) probably depends on these factors. After cold winters the densities of invertebrates are lower and, as a result, the food supply for foraging birds is lower. Thus, when the Dunlins arrive in spring, they may encounter quite different amounts of food in different years, which could influence their reproductive decisions.

In the area where Dunlins had their nests (the Northeast corner), the food supply was scarce when the birds arrived in spring. The number of invertebrates decreased until the end of May, when the Dunlins started to reproduce. The patterns were almost identical in the Pond. The decrease in food supply is probably caused by predation from birds and fish, which were foraging in the shallow water and on the exposed mud flats. This type of variation is common in areas with shallow water (Möller et al.1984).

In the more marine habitats (the Bay and the Southern bay), the food supply was much richer, being dominated by the amphipod crustacean *Corophium volutator* and the polychaete worm *Hediste diversicolor*. The prey numbers and biomass increased over the spring as crustaceans and polychaete worms started to reproduce (Muus 1967, Jensen 1988).

To summarise, food was scarce close to the nesting area in the pastures when the Dunlins arrived in spring. In contrast, in the marine habitats the food supply increased gradually during spring. Most marine invertebrates were not accessible for Dunlins during periods with low atmospheric pressure and high water level, but they were forced to switch to the Pond when high water levels made foraging impossible in the marine areas. Thus, the food supply for the Dunlins was probably influenced by both availability of prey and accessibility of good foraging sites.

In 1995, the Dunlins produced significantly larger eggs than in 1996. The decline in egg size in 1996 can be related to markedly lower food supply that year which would be in accordance with our first prediction. The difference in food supply between 1995 and 1997 was also considerable, especially in terms of prey biomass. This difference, however, did not translate into a difference in egg volume between these two years. A possible explanation for this may be that food supply was rich enough both these years not to limit egg-size, as egg volume may be limited by other factors when food is abundant (Grønstøl 1997). Most of the studies concerning the food supply for birds in the breeding season suggest that there is no lack of food (reviewed in Martin 1987). Thus, it is perhaps only under rather unfavourable conditions that the egg size is limited by insufficient food, and such conditions may only have occurred in 1996.

The abundance of food increased during spring. Compared to mid April 1995, the biomass was 150% greater a month later in the Bay. This increase in food supply did not result in an increase in egg volume, which is contrary to our prediction. Other studies have shown that egg size is correlated to the food supply, larger eggs being produced when the food supply increases (Bancroft 1984) and smaller egg size when the food supply decreases (Mills 1979). For arctic waders, a negative correlation between egg volume and the dates of clutch initiation have been observed (Byrkjedal & Kålås 1985, Sandercock et al. 1999). In these studies, the most plausible explanation was that this depended on the age and quality of the parents, i.e. older females of higher quality breeding earlier in the season and producing larger eggs.

In spite of greater food supply later in the season, egg size did not increase in our study of Dunlins. There are several possible reasons for this result. Female Dunlins in most cases leave the breeding grounds long before their chicks are fledged and migrate to Western Europe where they moult (Jönsson 1986). There might be a trade-off between an early migration to the moulting area and waiting for a longer period at the breeding grounds before start of egg laying to be able to produce larger and more nutrient-rich eggs. In the Kentish Plover *Charadrius alexandrinus*, larger eggs take a longer time to produce (Amat et al. 2001). Another possible explanation is that it is a bad strategy to invest more time in producing large eggs late in the breeding season, because chicks from late clutches usually have lower survival rates (Soikkeli 1967, Daan et al. 1988, Perrins 1996; but see Lank et al. 1985, Wallander & Andersson 2003).

In summary, Dunlins had larger egg volumes in two years when the food supply was rich, and smaller egg volume in a year when food supply was much lower. We did not find any relationship between egg volume and food supply over the breeding season. This latter result could be a consequence of later females facing time constraints or that they invest less in late broods that have lower survival rates. However, later breeding females may also be of lower quality (and thus have a lower potential for egg volume investment), and that this factor was compensated by a seasonal increase in food supply..

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Sammanfattning

För många djur finns det ett positivt samband mellan äggstorleken och tillväxten eller överlevnaden hos ungarna (Williams 1994, Christians 2002). Orsakssammanhangen är dock oklara och flera försök har gjorts att skilja de effekter som stora ägg har på ungarnas överlevnad och tillväxt från effekter som beror på föräldrarnas egenskaper. De positiva effekterna av att komma från ett stort ägg kan vara kortvariga. För vadar- och trutungar från stora ägg har konstaterats högre överlevnad under första levnadsveckan (Parsons 1970, Galbraith 1988a, Grant 1991, Blomqvist et al 1997). Ungar från stora ägg har fördelar de första dagarna om kläckningen t.ex. sker vid dålig väderlek som försvårar deras möjligheter att söka föda.

För tofsvipor *Vanellus vanellus* har visats att honor som söker föda i rikare områden producerar större ägg (Galbraith 1988b, Blomqvist & Johansson 1995). Detta förhållande gäller dock inte alltid. När näringstillgången är mycket god samvarierar inte näringstillgång och äggstorlek utan andra faktorer har jämförelsevis större effekt (Grønstøl 1997). Det kan alltså finnas en viss nivå över vilken näringstillgången inte längre påverkar äggvolymen. Erckmann (1983) visade att vadarhonors vikt är ungefär den samma före och efter äggläggningen. Vadare är i så fall i hög grad beroende av näringstillgången på häckningsplatsen för äggbildning och förändringar i näringstillgången bör därför avspegla sig i variationer i äggvolym hos arter som t.ex. den sydliga rasen av kärrsnäppa *Calidris alpina schinzii.*

I vår studie har vi undersökt sambandet mellan födotillgång och äggstorlek hos kärrsnäppa som häckar på havsstrandängar i södra Sverige. Vi testade särskilt två förutsägelser som bör gälla om näringstillgången är på en kritisk nivå för produktion av ägg: (1) Äggvolymen följer variationer i näringstillgång mellan olika år och (2) äggvolymen ändras om näringstillgången ökar eller minskar under häckningssäsongen.

Studien utfördes från slutet av mars till slutet av juni 1995–1997 och bedrevs i huvudsak inom Getteröns naturreservat på den svenska västkusten. En studie av kärrsnäppor pågår sedan flera år på Västkusten och större delen av Getteröns kärrsnäppor är därför märkta med individuella färgringskombinationer (Blomqvist och Johansson 1991). Merparten av kärrsnäppebona är belägna inom ett något mindre än 20 ha stort gräsmarksområde (Figur1) i reservatets nordöstra delar (*NO hörnet*). Under våren, före äggläggningen, födosöker kärrsnäpporna på tre platser (Figur 1): (1) Utmed kanten på den konstgjorda dammen (*Dammen*) där vattenståndet är stabilt, (2) Söder om Getterövägen (utanför reservatet) i *Södra viken* och i (3) Den yttre Farehamnviken (*Viken*).

Antalet kärrsnäppor registrerades och färgringskombinationerna avlästes när kärrsnäpporna anlände på våren. Nästa steg var att söka efter bon och identifiera de adulta fåglarnas ringkombinationer. Tiden som äggen ruvats bestämdes genom att undersöka äggens flytförmåga (van Paassen m.fl. 1984, Blomqvist 1996).Äggen mättes med metod enligt Väisänen (1977). Vi anger äggvolymen som medeläggvolymen för respektive kull.

För att bestämma mängden näring som var tillgänglig för kärrsnäpporna studerades bottenfaunan på de tre platserna (se ovan) som vanligtvis utnyttjades av födosökande kärrsnäppor samt i anslutning till deras häckningsplats. Biomassan anges som askfri torrvikt (AFDW). Vid analyserna av födotillgång har vi inkluderat enbart djur som rapporterats som bytesdjur för kärrsnäppa (Norlin 1965, Bengtsson & Svensson 1968, Glutz von Blotzheim et al. 1975 , Cramp & Simmons 1983).

Vi inventerade födosökande kärrsnäppor under 1997 och totalt gjordes 171 observationer av födosökande kärrsnäppeindivider. Vid lågt vattenstånd födosökte kärrsnäpporna på de blottlagda bankarna i Viken och Södra-viken, medan de vid högt vattenstånd var hänvisade till Dammen. Kärrsnäppeflocken försvann regelbundet ut på öarna väster om Getterön.

Variation i bytestillgång mellan år

Antal potentiella bytesdjur och bytesbiomassan i de olika födosöksområdena visas i Tabell 1. I Viken fann vi signifikanta skillnader i förekomst av bottendjur mellan 1995 och de båda efterföljande åren, medan dessa skillnader inte var statistiskt signifikanta mellan 1996 och 1997. I Dammen var det en signifikant skillnad mellan 1995 och de båda efterföljande åren för både antal byten och deras biomassa. Mellan 1996 och 1997 var dessa skillnader dock inte signifikanta. Vattensamlingarna vid kärrsnäppornas häckningsplats (*NO-hörnet*) uppvisade likheter med Viken och Dammen. Mellan 1995 och 1996 var minskningen signifikant både för antal byten och deras biomassa, medan det mellan 1996 och 1997 skedde en signifikant ökning. I jämförelse med de övriga platserna var bytesdjurens biomassa dock väsentligt lägre i NO-hörnet (Tabell1). I Södra viken var bottenfaunan mer varierad. I motsats till de andra områdena fanns inga signifikanta skillnader i antal potentiella bytesdjur mellan åren. För bytesdjurens biomassa var skillnaderna däremot tydliga, med en signifikant minskning mellan 1995 och 1996, men däremot inte mellan 1996 och 1997.

Variation i bytestillgång under häckningssäsongen 1995

Näringtillgången under våren föreföll inte att samvariera på de fyra provtagningsplatserna (Tabell 2). När det gäller den marina miljön i Södra viken fanns det skillnader mellan de tre provtillfällena. Mellan april och maj var skillnaden signifikant, vilket den dock inte var mellan maj och juni. För biomassan var förhållandet likartat med signifikanta skillnader mellan provtillfällena och signifikant ökning mellan april och maj, men däremot inte mellan maj och juni. I Dammen, med bräckt vattnet, var det klara förändringar både i antalet bytesdjur och deras biomassa. Antalet bytesdjur och bytesbiomassan minskade signifikant från april till maj, för att sedan visa en ickesignifikant tendens till att öka från maj till juni. I NO-hörnet följde variationerna delvis samma mönster som i Dammen både för bytesantal och biomassa. Minskningen mellan april och maj var dock ej signifikant, medan ökningen mellan maj och juni var signifikant för både biomassa och antal.

Äggvolym

Medeläggvolymen skiljde sig signifikant åt mellan 1995–1996 och 1996–1997. Däremot fanns ingen skillnad i äggvolym över säsongen under perioden 26/4 till 27/5 1995, trots att näringstillgången ökade under denna period.

Diskussion

Näringstillgången var liten i anslutning till häckningsplatserna på strandängarna (NO-hörnet och Dammen). I havsvikarna (Viken och Södra Viken) var näringstillgången hög och havsvikarna de viktigaste födosöksplatserna på våren. Kärrsnäpporna blev dock hänvisade till Dammen då hög vattennivå omöjliggjorde födosök i havsvikarna. Tillgången på näring reglerades därför både av förekomst och tillgänglighet.

Under 1995 producerade kärrsnäpporna signifikant större ägg jämfört med 1996. Detta kan förklaras av att det var en högre tillgång på näring och större tillgänglighet till de bra födosöksplatserna 1995. Skillnaden i näringstillgång mellan 1995 och 1997 var också stor, speciellt när det gäller biomassan men skillnaden i äggvolym mellan de båda åren var inte signifikant. Detta kan kanske förklaras med att både under 1995 och 1997 var näringstillgången så god att den var över den gräns där dålig födotillgången påverkar äggvolymen negativt. Under sådana förhållanden är det istället andra faktorer som har större effekt på äggstorleken (Grønstøl 1997). Däremot kan den låga födotillgången 1996 ha varit under den kritiska nivån då näringsbrist leder till produktion av ägg med mindre volym.

I vår studie ökade näringtillgången under våren men detta resulterade dock inte i någon ökning av äggvolymen. Detta står i motsats till andra undersökningar som visat att äggvolymen ökar vid ökad näringstillgång (Bancroft 1984) och att den minskar vid minskad näringstillgång (Mills 1979). För arktiska vadare rapporterades minskad äggstorlek under häckningssäsongens lopp (Byrkjedal & Kålås 1985, Sandercock et al. 1999). Orsaken till den minskande äggvolymen är oklar. Föräldrarnas ålder och kvalité var troliga orsaker, d.v.s. att äldre och mer högkvalitativa honor lägger större ägg tidigare på säsongen. Sandercock et al. (1999) spekulerade i att honorna anländer till häckningsplatserna med begränsade näringsreserver som successivt förbrukas vid normal ämnesomsättning och därmed ger mindre näring till äggproduktion senare på säsongen. Förhållanden med näringsbrist på häckningsplatsen torde dock i första hand gälla för arktiska arter. I vårt material kan vi dock inte se några förändringar i äggvolymen under säsongen 1995 och förklaringen är kanske densamma som ovan: näringstillgången var under 1995 hög redan tidigt under våren. Någon betydande näringsbrist uppstod inte och därmed påverkades inte äggvolymen.

Att äggstorleken, trots en större näringstillgången, inte ökade under säsongen kan förklaras på flera sätt. Kärrsnäppehonorna lämnar i de flesta fall häckningsplatsen långt före ungarna blivit flygga och flyttar till Västeuropas kuster där de ruggar (Jönsson 1986). Det kan då finnas en avvägning mellan att flytta tidigt till ruggningslokalerna och att stanna kvar längre så att de kan lägga större och mer energikrävande ägg. Större ägg tar, åtminstone för svartbent strandpipare *Charadrius alexandrinus*, längre tid att producera (Amat m.fl. 2001), och det är fullt tänkbart att samma sak gäller för kärrsnäppa. En annan förklaring är att det inte lönar sig att investera i stora ägg sent på säsongen eftersom ungar från sena kullar vanligen har sämre överlevnad (Soikkeli 1967, Daan et al. 1988, Perrins 1996; men se Lank et al. 1985, Wallander & Andersson 2003).