ORIGINAL ARTICLE

Survival during the pre-fledging period rather than during post-fledging drives variation in local recruitment of an endangered migratory shorebird, the Southern Dunlin *Calidris alpina schinzii*

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Abstract

The declines in wet-grassland breeding shorebird populations are considered to mainly result from changes in reproduction. While there is plenty of information on nest survival, little reliable information exists on local recruitment due to confounding effects of permanent emigration. Furthermore, few studies have been able to study the roles of pre- and post-fledging survival on local recruitment. Therefore, it is unclear whether local recruitment of young reflects conditions at the breeding sites or at non-breeding sites. We studied an isolated population of the endangered Southern Dunlin (*Calidris alpina schinzii*) breeding on the west coast of Sweden to examine (1) brood survival (probability of at least one chick fledging) by following broods fates and (2) local recruitment (survival from hatching to 1 year old) using capture-recapture data. We then examined how much of the annual variation in juvenile survival was explained by variation in brood survival. Brood survival was on average 0.58 (annual range 0.08–1.00) and explained 64% of variation in annual local recruitment. Still local recruitment was rather high for a shorebird (0.17, SE = 0.023), which reflects the isolated nature of the study population. Our results suggest that local recruitment seems to be mainly constrained by chick survival during the pre-fledging period. Therefore, management of breeding sites leading to increased brood survival, e.g., reducing predation on chicks, should have strong impacts on local recruitment and local population growth.

Keywords Baltic dunlin · Capture-recapture · Juvenile survival · Precocial · Shorebird

Zusammenfassung

Das Überleben vor, nicht nach dem Flüggewerden führt bei einem bedrohten Küstenzugvogel, dem Südlichen Alpenstrandläufer *(Calidris alpina schinzii),* **zu Unterschieden in der Ortstreue der Jungtiere**
Man geht davon aus, dass der Rückgang der in Feuchtwiesen brütenden Küstenvogelpopulationen in erster Linie auf Veränderungen in der Fortpflanzung zurückzuführen ist. Zwar gibt es viele Ergebnisse zum Überleben im Nest, aber aufgrund der verzerrenden Effekte durch viele Abwandernde, die dauerhaft wegbleiben, gibt es nur wenig zuverlässige Informationen über die ortstreuen Tiere. Außerdem konnten nur wenige Studien die Auswirkungen des Überlebens vor und nach dem Flüggewerden auf die Ortstreue untersuchen. Deshalb ist unklar, ob die die Ortstreue der Jungen von den Verhältnissen am Brutplatz oder von denen an anderen Orten, an denen nicht gebrütet wird, abhängt. Wir untersuchten an einer isoliert lebenden Population des Südlichen Alpenstrandläufers (*Calidris alpina schinzii*), der an der schwedischen Westküste brütet,

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1) das Überleben der Brut (Wahrscheinlichkeit, dass wenigstens ein Tier ausfliegt), indem wir das weitere Schicksal der Brut verfolgten, und 2) die Ortstreue anhand von Wiederfangsdaten (Überlebende vom Schlüpfen bis zum Alter von einem Jahr). Wir überprüften anhand dieser Informationen, wie viel der jährlichen Unterschiede im Überleben der Jungtiere mit den Unterschieden im Überleben der Brut erklärt werden konnte. Die Überlebensrate der Brut betrug im Mittel 0,58 (die Spanne eines Jahres reichte von 0,08 bis 1,00) und konnte 64% der Unterschiede in der jährlichen Ortstreue erklären. Für einen Küstenvogel war die Ortstreue ziemlich hoch (0,17, SE = 0,023), was die isolierte Lage der von uns untersuchten Population widerspiegelt. Unsere Ergebnisse deuten darauf hin, dass die Ortstreue hauptsächlich vom Überleben der Küken in der Zeit vor dem Flüggewerden begrenzt wird. Deshalb müsste ein Management von Brutplätzen, das z.B. durch die Verringerung von Ausfällen durch Räuber zu einer erhöhten Überlebensrate der Brut führte, einen großen Einfluss auf die Ortstreue und das Wachstum der Population an dem Ort haben.

Introduction

Successful conservation of endangered populations requires detailed information on factors affecting the life history traits that determine the population growth rate. Shorebird populations breeding on wet grasslands have been declining in the last decades within Europe (e.g., Thorup 2006). The population declines have been attributed to changes in reproduction rather than adult survival (e.g., Roodbergen et al. 2012; Pakanen and Thorup 2016; Plard et al. 2020). Habitat changes and increased nest predation in particular have been suggested as the driving forces behind these declines (e.g., Rönkä et al. 2006; Roodbergen et al. 2012). Importantly, reproduction can be partitioned into nest survival, number of hatched young and local recruitment, but solid knowledge about the latter is relatively scarce. This is because local recruitment is the proportion of individuals that survive and return to their natal population, and permanent emigration caused by natal dispersal may bias estimates (Paradis et al. 1998). This constitutes an important lack in our understanding of population dynamics and potential management options in species such as shorebirds, as local recruitment, i.e., juvenile survival, can have a strong contribution to population growth rate (Saether and Bakke 2000). Furthermore, as juvenile survival is determined by pre-fledging and post-fledging conditions, it can be difficult to assess whether juvenile survival reflects conditions at the breeding sites or at non-breeding sites. Mortality is often highest early in life (e.g., Caughley 1966; Sullivan 1989; Stearns 1992). However, studying pre-fledging survival of precocial species is difficult and therefore few long-term studies have been able to study the relative roles of pre- and post-fledging survival on local recruitment in such species (Roodbergen et al. 2012).

Here, we examine chick survival in the endangered Southern dunlin (*Calidris alpina schinzii*), using long-term data from a breeding population on the west coast of Sweden (e.g., Blomqvist et al. 2010). Firstly, we followed broods from hatching until fledging or brood disappearance to estimate annual variation in the probability of at least one chick fledging (hereafter termed brood survival). Secondly, we used capture-recapture models to estimate local recruitment, i.e., survival from hatching to the age of 1 year. Finally, we examined how much of the annual variation in juvenile survival that is explained by variation in brood survival. While brood survival and juvenile survival can be expected to be correlated, their level of correlation will be low if juvenile survival is mainly affected by conditions at the non-breeding sites. In contrast, the correlation should be stronger if juvenile survival is mainly determined by factors operating at the breeding sites. For example, juvenile survival can be low if post-fledging survival is low despite high pre-fledging survival, whereas juvenile survival will always be low if pre-fledging survival is low. The study population is isolated from other populations with the nearest breeding population being about 300 km away from our study population in the province of Scania, SW Sweden (Blomqvist et al. 2010). Due to the isolation from other populations, and because all known breeding sites are monitored regularly, and dispersal between the sites is rare and controlled for, we were able to reliably estimate local recruitment (Pakanen et al. 2017).

Materials and methods

We studied Southern Dunlins on the west coast of Sweden (57°55′N, 11°47E–57°7′N, 12°14′E); here we examine chick survival at five coastal meadows that have regularly held breeding Dunlins (Fig. 1). We restrict the analyses to the data collected 1990–2005 since our data on brood survival are limited before and after this period. We started fieldwork by searching for territories in early April and continued with searching for nests or broods until late June. We usually visited the breeding sites every 2–5 days, with more frequent visits to the larger breeding sites and generally longer monitoring intervals towards the end of the breeding season. We monitored the nests until they hatched or failed. Chicks were captured in or near the nest soon after hatching and ringed with a metal ring with a numerical code that was unique for each bird (in some years, chicks were also ringed with colour rings) provided by the Swedish bird ringing centre. Broods were followed
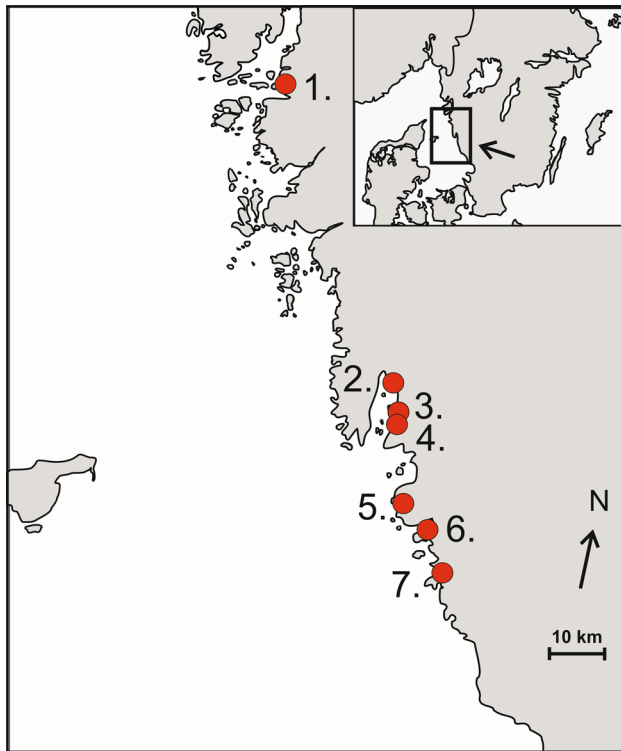
Fig. 1 Location of the breeding sites of Southern Dunlin on the west coast of Sweden (1 = Ödsmåls kile, 2 = Torkelstorp, 3 = Tjolöholm, 4 = Ölmevalla, 5 = Båtafjorden, 6 = Klosterfjorden, 7 = Getterön). See Pakanen et al. (2017) for further details on the sites; note that the breeding sites Klosterfjorden and Getterön were excluded from the analyses presented here due to insufficient data on brood survival

periodically every 2–3 days until the chicks were observed as fledglings (around 20 days after hatching) or they were at least 14 days old. Chick mortality is usually very low after this age (Blomqvist, unpubl.). The entire brood was considered dead if the chicks disappeared before they were 14 days old and the previously tending adults showed no parental behaviours on two or more occasions.

Data on local recruitment accumulated when the chicks recruited back to population to breed in later years. We caught them as breeding adults with cage traps when they were incubating eggs or brooding chicks. We ringed each adult with a unique, individual combination of colour rings that allowed us to identify them in subsequent years. More detailed field methods can be found elsewhere (Blomqvist and Johansson 1991; Pauliny et al. 2008; Blomqvist et al. 2010; Flodin and Blomqvist 2012). The final data included 129 broods and 359 chicks that were born between 1990 and 2005. The mean number of chicks per brood at hatching was 2.7. We pooled data from each site to calculate brood survival for each year as the proportion of broods that fledged at least one chick.

We examined juvenile survival with CJS models (the Cormack-Jolly-Seber model) in program MARK (White

and Burnham 1999). In this approach, individual encounter histories that summarise their observations from hatching until adulthood and until their disappearance across the different breeding seasons is used to estimate survival of individuals. The CJS model estimates survival (Φ) by correcting for the probability of recapture (p) that is estimated from the data. Our starting model [Φ(ac1t/ac2c) p(ac1t/ac2c)] included age class (ac: juveniles ac1 vs. adults ac2), but we kept survival and recapture probabilities constant in time for adults (ac2c) and time-dependent for juveniles (ac1t). This model fit the data (bootstrapping goodness of fit; $p = 0.18$, $\hat{c} = 1.149$). We then fitted models with constant survival and recapture probabilities for juveniles, and a covariate model that constrained juvenile survival to be a linear function of the brood survival estimate of that year. We compared models using QAICc values, which consider overdispersion and is corrected for small sample size (Burnham and Anderson 2002). To examine the relationship between temporal variation in brood survival and juvenile survival, we calculated the percentage of deviance explained by the annual covariate (cov) of brood survival as:

$$\frac{\text{Dev}_{(c)} - \text{Dev}_{(cov)}}{\text{Dev}_{(c)} - \text{Dev}_{(t)}},$$

where Dev(c) is the deviance from the constant model, Dev(cov) is deviance from the covariate model and Dev(t) is the deviance from the time-dependent model (Grosbois et al. 2008).

Results

Annual brood survival varied between 0.08 and 1.00 with an annual mean of 0.58 (SE = 0.067, $n = 16$; Fig. 2). The best model (ΔQAIC = 8.7) for juvenile survival was the covariate model showing a positive linear effect of brood survival on juvenile survival (Table 1; Fig. 3; $\beta_{\text{brood survival}} = 2.290$, CI 0.952–3.629 on the logit scale). Brood survival explained 64% of annual variation in juvenile survival (Fig. 3; ANODEV: $F = 24.35$, $df = 1$, $p < 0.001$). While annual variation in juvenile survival was not supported by the QAIC due to small sample sizes (Table 1, models A2 and A3), the annual estimates from the time-dependent model were clearly low in years of low brood survival and high in years of high brood survival (Fig. 2). Juvenile survival estimated from the constant model was 0.171 (SE = 0.023).
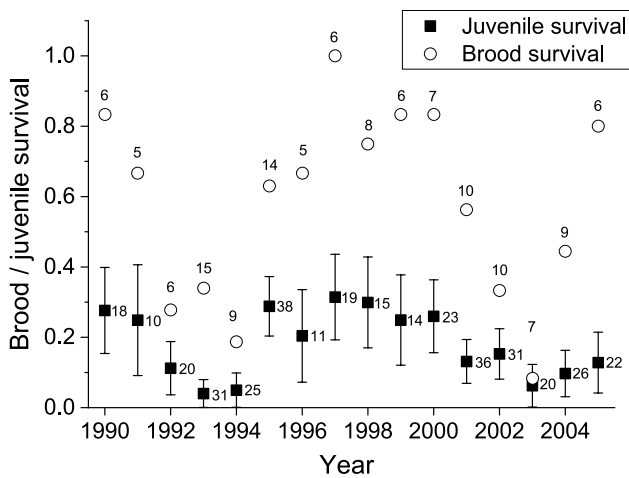
Fig. 2 Annual variation in the survival of broods and juveniles (± SE) of Southern Dunlin on the west coast of Sweden. Numbers indicate annual number of broods (brood survival) and the number of juveniles (juvenile survival)

Discussion

We followed 129 broods of the Southern Dunlin from hatching and found that 58% of them fledged at least one chick. This means that pre-fledging survival lies between 0.19–0.58 assuming 1–3 chicks fledging from a brood. Jönsson (1991) reported a fledging survival of 0.36 for Southern Dunlins breeding in southern Sweden. While studies on pre-fledging survival from comparable small shorebirds are rare, recent studies have reported a pre-fledging survival of 0.48 for the *arcticola* subspecies of the dunlin (until 15 days old; Hill 2012) and 0.39–0.65 for the Piping Plover (*Charadrius melanotos*; until 25 days old; Hunt et al. 2018). Because those pre-fledging survival estimates measure the probability of one chick surviving, brood survival in those cases were likely higher compared to brood survival in our population. A similar study to ours estimated brood survival of 0.73 for Western Sandpipers (*Calidris mauri*) in Alaska (Ruthrauff and McCaffery 2005). It seems therefore that pre-fledging survival may be comparatively low in temperate grasslands. Indeed, low pre-fledging survival has been reported from larger species such as Black-tailed Godwits (*Limosa*

limosa; 0.02–0.11; Salewski and Schütze 2017) and Lapwings (*Vanellus vanellus*; 0.18; Plard et al. 2020) breeding in Europe.

Average juvenile survival of Southern Dunlin in Sweden was 17%, which is slightly lower than apparent juvenile survival estimated from a Southern Dunlin population breeding at Bothnian Bay, Finland (20%, Pakanen et al. 2016) as well as in a population in southern Sweden (Skåne), where juvenile survival was estimated at 20.1% (Jönsson 1991). Notably, the latter estimate was derived using the return rate of juveniles (0.167) and assuming constant adult survival until the individuals were recruited (Jönsson 1991). The estimated survival rates for juvenile Southern Dunlins are rather high compared to other small shorebirds, in which the estimates often range between 0.05 and 0.1 because permanent emigration can occur due to available habitat elsewhere (Sandercock et al. 2005; Koivula et al. 2008; Nol et al. 2010; Pakanen et al. 2015). Since our study population shows little to no dispersal and because most of the possible breeding areas were included in the study (Fig. 1, Pakanen et al. 2017), our estimates can be considered to reliably reflect true survival. Given the apparently low pre-fledging survival, post-fledging survival needs to be rather high as the average juvenile survival, i.e., until 1 year old, was 0.17. Jönsson (1991)
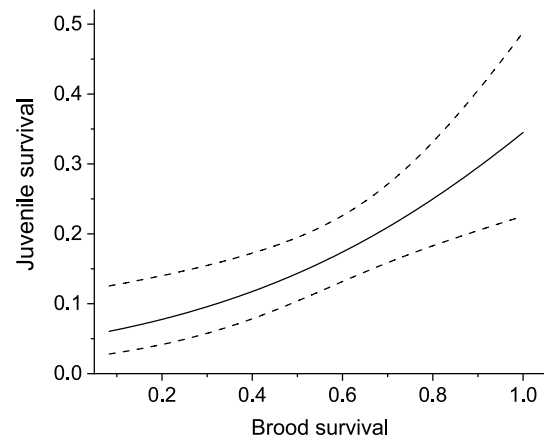

Fig. 3 The relationship between brood survival and juvenile survival in a Southern Dunlin population breeding on the west coast of Sweden as estimated from model A1 (Table 1)

Table 1 Models examining juvenile survival of Southern Dunlin ranked with QAICc

#	Model	QAICc	ΔQAICc	w	k	QDeviance
A1	Φ(ac1FLEDGE/ac2c) p(ac1c/ac2c)	596.5418	0.000	0.987	5	234.219
A2	Φ(ac1c/ac2c) p(ac1c/ac2c)	605.2694	8.728	0.013	4	244.983
A3	Φ(ac1t/ac2c) p(ac1c/ac2c)	619.6712	23.129	0.000	19	228.030
A4	Φ(ac1t/ac2c) p(ac1t/ac2c)	643.7937	47.252	0.000	34	218.977

ΔQAICc = QAICc(i) − QAICc(min), w = QAICc weight, k = number of parameters, t = time dependent, c = constant, aci = age class (i), FLEDGE = brood survival

estimated the post-fledging survival of Southern Dunlin as 0.556.

Our estimate of juvenile survival may be too low for maintaining a stable population given other demographic rates in this population. With an adult survival rate of 0.80 for females (Blomqvist unpublished data), nest success of 0.41 (Pauliny et al. 2008), renesting probability of 0.47 (Pakanen et al. 2014) and breeding probabilities that follow those published by Pakanen et al. (2016), juvenile survival from hatching to age one should be ~ 0.26 to keep the population stable. That is 50% higher than our estimate. This level of juvenile survival was achieved in some years during the study but not in most years (Fig. 2). Thus, low juvenile survival may likely have contributed to the decline of this population (see also Plard et al. 2020).

Annual brood survival estimates explained a large portion (64%) of temporal variation in local recruitment of an endangered Southern Dunlin population. This relationship was the result of extensive variation in brood survival. In some years, brood survival was very low, allowing very little local recruitment. Based on these results, local recruitment seems to be mainly constrained by the survival during the pre-fledging period. Therefore, management actions conducted at the breeding sites that increase brood survival should have strong impacts on local recruitment. Given the rapid decline of the Baltic population of Southern Dunlin, there is a dire need for effective management that increases survival of broods. This lack of information applies to all grassland breeding species (Franks et al. 2018). Their survival can be different in different habitats; lower due to agricultural activities, low food availability or harsh weather conditions (Groen and Hemerik 2002; Lengyel 2006; Kentie et al. 2013; Ackerman et al. 2014; Machin et al. 2018). In our study population, inbreeding also affects the viability of juveniles (Blomqvist et al. 2010; see also Pauliny et al. 2008), which may be reflected in the lower survival rates especially towards the last years of the study (Fig. 2). Nevertheless, most mortality of shorebird chicks occurs through predation (Mason et al. 2018). Thus, direct predator control can be very effective (Rickenbach et al. 2011), but it requires substantial efforts that are not possible at a large scale. Therefore, identifying the habitat characteristics that lead to increased predation of chicks may lead to the most successful management options.

Compliance with ethical standards

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