

Age-specific reproductive performance in Citril Finches *Carduelis [citrinella]*

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We studied age-specific reproductive performance of subadult (2nd calendar year) and adult (3rd calendar year or older) Citril Finches *Carduelis [citrinella]* in several sub-populations of the species (Black Forest, SW Germany; Pyrenees, NE Spain; Corsica, France; Sardinia, Italy). In accordance with the results of many other studies we hypothesised to find an increase in reproductive success with age due to higher experience of older birds. As expected we found significantly higher nesting success in experienced pairs (two adult birds) than in pairs with the participation of at least one subadult bird. Individual breeding performance revealed similar results with considerably higher breeding and nesting success for adult than for subadult males and females. We suggest therefore that adult Citril Finches appear to perform much better than subadult birds, probably due to higher experience in foraging and the acquirement of high quality habitats. Our data let us conclude that the first year in Citril Finch lifetime history seems to be rather unproductive. We suppose that subadult Citril Finches use this first year to gain necessary skills for nest building and optimal food selection to breed successfully in the following years. Their lifetime history may be therefore aligned with longer life span due to a longer learning curve than in comparable species such as Siskins *Carduelis spinus*, which possess a much faster turnover in their reproduction cycle.

Key words: reproductive success, foraging skills, age-effects

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Introduction

Reproductive performance of birds may vary considerably during their lifetime (Newton 1989). Many studies have shown that reproductive success improves with age, affecting breeding date and the number of offspring (Orlans & Beletsky 1989, Saether 1990, Forslund & Pärt 1995, Komdeur 1996, Newton & Rothery 1997, Espie *et al.* 2000, Robertson & Rendell 2001, Wiklander *et al.* 2001, Laaksonen *et al.* 2002, Nielsen & Drach-

mann 2003). However, increased reproductive success due to age has not been confirmed in all studies (McCleery & Perrins 1989, Payne 1989).

It is known that the improvement of the reproductive performance with age is mainly linked to higher foraging efficiency and to an increase in access to high quality mates and territories (Curio 1983, Nol & Smith 1987, Pietiäinen 1988, Komdeur 1996, Pärt 2001, Zanette 2001, Reid *et al.* 2003). Reproductive success may increase because an

individual's optimal level of reproductive effort rises with age due to changes in reproductive costs or residual reproductive value (Williams 1966, Pianka & Parker 1975, Clutton-Brock 1988). In Choughs *Pyrrhocorax pyrrhocorax* for example, mean reproductive performance improves from young to middle-aged birds because individual females lay larger clutches, are less likely to fail and fledge more offspring (Reid *et al.* 2003). In this context in many bird species normally a bell-shaped relationship between female age and reproduction occurs, where performance peaks in middle age rather than at the onset of reproduction (Clutton-Brock 1988, Komdeur 1996, Newton & Rothery 1997, Robertson & Rendell 2001, Reid *et al.* 2003).

Our study object, the Citril Finch *Carduelis [citrinella]* lives as an endemic bird species in the montane and subalpine mountain zones of the Western and Central Palearctic and is drawn to conifer forests (Cramp & Perrins 1994). Similar to other Carduelid finches it breeds mainly in neighbourhood groups (Förschler 2002). Between 1999 and 2003 we studied breeding ecology of Citril Finches all over the species' small range at four distinct breeding sites: Black Forest (SW Germany), Pyrenees (NE Spain), Corsica (France), Sardinia (Italy) (Förschler & Kalko 2006b). In this context it was possible to gather information on age-specific breeding success at all these sites. Age of nesting individuals was determined by observations with binoculars and by means of typical plumage marks during nest building phase. Subadult birds of 2nd calendar year and adult birds of 3rd calendar year or older may be distinguished under good observation conditions accurately by the whitish (instead of yellow) coloration of several greater wing coverts (Bezzel 1993, Clement *et al.* 1993, Jenni & Winkler 1994, Glutz von Blotzheim & Bauer 1997).

Citril Finches in their first breeding year appear not to contribute significantly to the number of offspring in a population (pers. obs.). Subadult or juvenile Citril Finches lack specific knowledge and information on the most important food plants necessary for successful breeding (Förschler & Kalko 2006a), and younger birds may be ousted

into lower quality habitats (Förschler 2002). In accordance with other studies (see above) we hypothesise an increase in breeding success with age due to an increase in experience of older birds. In this study we therefore tested for differences in reproductive performance between subadult and adult Citril Finches.

Results

We determined the ages of Citril Finch nesting pairs and scored two age classes: subadult or adult. In 66% of all age-determined pairs ($n = 83$) we registered pairs in which both partners were adult. Almost a third of the pairs (27%) were composed of two 2nd calendar year (subadult) birds. In a few cases (7%), an adult male was found to nest with a subadult female and we never observed any pairs consisting of a subadult male with an adult female. It was not always possible to determine the age of both members of a breeding pair. Therefore we present more data on the performance of individuals mated to a partner of unknown age (Table 2) than on the performance of pairs of which both members could be aged (Table 1).

We pooled data of the four study sites for analysing age-specific reproductive performance. Age distribution of males, females and pair combinations did not differ between study sites (General Nonlinear Model, all $P > 0.2$). We compared clutch size, hatching, breeding and nesting success. Hatching success was defined as number of young in relation to total number of eggs per nest; breeding success refers to the number of fledglings in relation to total number of eggs, and nesting success represents the number of nests with at least one fledgling in relation to total number of nests (Bairlein 1996). While clutch size and hatching did not differ, we found a considerable (but not significant) lower breeding success in pairs with a subadult female (22%) than in pairs consisting of two adult birds (43%). However we found a significant higher nesting success in adult-adult pairs (52%) than in pairs where a subadult female participated (9%) (Table 1).

Considering the individuals mated to a partner of unknown age, subadult and adult females

showed no significant differences in clutch size and hatching success. Breeding success was lower in subadult than adult females, although the difference was not significant. Nesting success was significantly lower however in subadult females: 16% of the subadult females had at least one fledgling in contrast to 53% in adult females (Table 2). In males, subadult males had a significantly lower breeding success (12%) than adult males (52%). Clutch sizes and hatching success of the associated females did not differ (Table 2). Similarly to adult females, adult males had a significantly higher nesting success (52%), while in subadult males this was only 10% (Table 2).

Discussion

In two thirds of all cases both mates of Citril Finch were adult individuals. In the other third, both mates were subadult birds or more rarely the male was an adult and the female a subadult bird. An adult female was never seen with a subadult mate, indicating that adult females were selectively choosing older and more experienced males. In concordance with this observation, we observed that a large portion of subadult males was not involved at all in breeding activity in their second year of life, e.g. at Monte Limbara and Monte Padorzu in Sardinia and in the mountains of Haut-Asco and Niolo in Corsica in 2001 (pers. obs.).

Table 1. Age-related reproductive performance in pairs of Citril Finches. Age of both partners was determined. Compared are breeding pairs with and without adult females. Clutch sizes and absolute hatching, breeding and nesting success are given (see text for definitions). Data were analysed by Mann-Whitney U-tests (with test-statistic T) for non-parametric data. For comparison of nesting success χ^2 -tests were used.

	Pairs consisting of adult males and adult females	Pairs with participation of subadult females	Comparison
Clutch size (mean $\pm$ SD)	3.82 $\pm$ 0.77 ($n = 28$)	3.78 $\pm$ 0.83 ($n = 9$)	$T = 172.0$, $P = 0.986$
Hatching success	53% ($n = 28$)	52% ($n = 9$)	$T = 170.5$, $P = 1.00$
Breeding success	43% ($n = 28$)	22% ($n = 9$)	$T = 138.5$, $P = 0.256$
Nesting success	52% ($n = 44$)	9% ($n = 23$)	$\chi^2_1 = 10.47$, $P = 0.001$

Table 2. Age-related reproductive performance of individual Citril Finches mated to partner of unknown age. Clutch sizes and absolute hatching, breeding and nesting success are given (see text for definitions). Data were analysed by Mann-Whitney U-tests (with test-statistic T) for non-parametric data. For comparison of nesting success χ^2 -tests were used.

	Adult males	Subadult males	Comparison
Clutch size (mean $\pm$ SD)	4.00 $\pm$ 0.81 ($n = 41$)	4.09 $\pm$ 0.83 ($n = 11$)	$T = 311.5$, $P = 0.66$
Hatching success	61% ($n = 41$)	55% ($n = 11$)	$T = 270.5$, $P = 0.65$
Breeding success	52% ($n = 41$)	12% ($n = 11$)	$T = 181.0$, $P = 0.01$
Nesting success	52% ($n = 65$)	10% ($n = 21$)	$\chi^2_1 = 10.24$, $P = 0.001$

	Adult females	Subadult females	Comparison
Clutch size (mean $\pm$ SD)	3.78 $\pm$ 0.83 ($n = 32$)	3.73 $\pm$ 0.79 ($n = 11$)	$T = 238.5$, $P = 0.93$
Hatching success	53% ($n = 32$)	61% ($n = 11$)	$T = 262.5$, $P = 0.58$
Breeding success	44% ($n = 32$)	36% ($n = 11$)	$T = 225.0$, $P = 0.65$
Nesting success	53% ($n = 49$)	16% ($n = 25$)	$\chi^2_1 = 17.96$, $P = 0.005$

As expected we found differences in reproductive performance between subadult and adult birds in our Citril Finch study populations. While clutch size and hatching success was similar for both groups, nesting success was significantly higher in adult-adult pair combinations than in subadult-adult and subadult-subadult pair combinations. Breeding performance in pairs with only one individual of known age revealed similar results, with considerably higher breeding and nesting success for adult than for subadult males and females.

Therefore, we suggest that adult birds appear to perform better than subadult birds, probably due to their previously gathered experience in foraging and their acquirement of high quality habitats and territories (Glück 1986, Pärt 2001, Zanette 2001, Reid *et al.* 2003). Furthermore the eggs and the young of subadult Citril Finches might be more often victims of predation (especially Jays *Garrulus glandarius*) and starvation due to bad weather periods (Förschler *et al.* 2005).

The fact that clutch size and hatching success did not show significant differences between adult and subadult females in contrast to nesting success, indicates that subadult Citril Finch females may be able to build nests, lay an appropriate number of eggs and even hatch them, but do not succeed in raising their offspring as well as do adult females. Probably subadult females also get lower quality mates such as subadult males or subordinate adult males with lower fitness, which enhances unsuccessful nesting.

Our data provides information that the first year in Citril Finch lifetime history seems to be a rather unproductive one. We suppose that young subadult birds use this first year to gain the necessary skills such as knowledge of nest building (Förschler 2002) and optimal food selection (Förschler & Kalko 2006a) for successful brood rearing in the following years. Lifetime history of Citril Finches may be therefore aligned with longer life span due to a longer learning curve for food acquirement skills than in comparable species such as Siskins *Carduelis spinus* (and maybe also Crossbills *Loxia curvirostra*), which possess a fast turnover in their reproduction cycle with early

breeding in young age classes, very low annual survival rates (Senar *et al.* 1993) and high annual variations in recruitment due to food source availability (Förschler *et al.* 2006).

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REFERENCES

- Bairlein F. 1996. Ökologie der Vögel. Fischer-Verlag, Stuttgart.
- Bezzel E. 1993. Kompendium der Vögel Mitteleuropas. Aula-Verlag, Wiesbaden.
- Clement P., Harris A. & Davis J. 1993. Finches & Sparrows. Helm Identification Guides, Singapore.
- Clutton-Brock T.H. 1988. Reproductive Success. University of Chicago Press, Chicago.
- Cramp S. & Perrins C.M. 1994. The birds of the western Palearctic. Vol. 8. Oxford University Press, Oxford.
- Curio E. 1983. Why do young birds reproduce less well? *Ibis* 125: 400–404.
- Espie R.H.M., Oliphant L.W., James P.C., Warkentin I.G. & Lieske D.J. 2000. Age-dependent breeding performance in merlins (*Falco columbarius*). *Ecology* 81: 3404–3415.
- Forslund P. & Pärt T. 1995. Age and reproduction in birds –hypotheses and tests. *Trends Ecol. Evol.* 10: 374–378.
- Förschler M.I. 2002. Brutbiologie des Zitronengirlitzes *Serinus citrinella* im Nordschwarzwald. *Ornithol. Beob.* 99: 19–32.
- Förschler M.I., Borrás A., Cabrera J., Cabrera T. & Senar J.C. 2005. Inter-locality variation in reproductive success of the Citril Finch *Serinus citrinella*. *J. Ornithol.* 146: 137–140.
- Förschler M.I. & Kalko E.K.V. 2006a. Macrogeographic variations in food choice of mainland Citril Finches

- Carduelis [citrinella] citrinella* versus insular Corsican (citril) finches *Carduelis [citrinella] corsicanus*. J. Ornithol. 147: 441–447.
- Förschler M.I., Kalko E.K.V. 2006b. Breeding ecology and nest site selection in allopatric mainland Citril Finches *Carduelis [citrinella] citrinella* and insular Corsican finches *Carduelis [citrinella] corsicanus*. J. Ornithol. doi: 10.1007/s10336-006-0079-z.
- Förschler M.I., Förschler L. & Dorka U. 2006. Flowe-ring intensity of spruces *Picea abies* and the population dynamics of siskins *Carduelis spinus*, common crossbills *Loxia curvirostra*, and Citril Finches *Carduelis citrinella*. Ornithol. Fenn. 83: 91–96.
- Glück E. 1986. Flock size and habitat-dependent food and energy intake of foraging Goldfinches. Oecologia 71: 149–155.
- Glutz von Blotzheim U.N. & Bauer K.M. 1997. Handbuch der Vögel Mitteleuropas. Vol. 14. Aula-Verlag, Wiesbaden.
- Jenni L. & Winkler R. 1994. Moults and ageing of European passerines. Academic Press, London.
- Komdeur J. 1996. Influence of age on reproductive performance in the Seychelles warbler. Behav. Ecol. 7: 417–425.
- Laaksonen T., Korpimäki E. & Hakkarainen H. 2002. Interactive effects of parental age and environmental variation on the breeding performance of Tengmalm's owls. J. Anim. Ecol. 71: 23–31.
- McCleery R.H. & Perrins C.M. 1989. Great Tit. In: Newton I. (ed) Lifetime reproduction in birds. Academic Press, London.
- Newton I. (ed) 1989. Lifetime reproductive success in birds. Academic Press, London.
- Newton I. & Rothery P. 1997. Senescence and reproductive value in sparrowhawks. Ecology 78: 1000–1008.
- Nielsen J.T. & Drachmann J. 2003. Age-dependent reproductive performance in Northern goshawks *Accipiter gentilis*. Ibis 145: 1–8.
- Nol E. & Smith J.N.M. 1987. Effects of age and breeding experience on seasonal reproductive success in the song sparrow. J. Anim. Ecol. 56: 301–313.
- Orians G.H. & Beletsky L.D. 1989. Red-winged blackbird. In: Newton I. (ed) Lifetime reproduction in birds. Academic Press, London.
- Pärt T. 2001. Experimental evidence of environmental effects on age-specific reproductive success: the importance of resource quality. Proc. R. Soc. London B 268: 2267–2271.
- Payne R.B. 1989. Indigo bunting. In: Newton I. (ed) Lifetime reproduction in birds. Academic Press, London.
- Pianka E.R. & Parker W.S. 1975. Age-specific reproductive tactics. Am. Nat. 360: 113–117.
- Pietiäinen H. 1988. Breeding season quality, age, and the effect of experience on the reproductive success of the Ural owl (*Strix uralensis*). Auk 105: 316–324.
- Reid J.M., Bignal E.M., Bignal S., McCracken D.I. & Monaghan P. 2003. Age-specific reproductive performance in red-billed choughs *Pyrrhonorax pyrrhonorax*: patterns and processes in natural population. J. Anim. Ecol. 72: 765–776.
- Robertson R.J. & Rendell W.B. 2001. A long-term study of reproductive performance in tree swallows: the influence of age and senescence on output. J. Anim. Ecol. 70: 1014–1031.
- Saether B.E. 1990. Age-specific variation in the reproductive performance of birds. Curr. Ornithol. 7: 251–283.
- Senar J.C., Borrás A., Cabrera T. & Cabrera J. 1993. Testing for the relationship between coniferous crop stability and common crossbill residence. J. Field Ornithol. 64: 464–469.
- Wiktander U., Olsson O. & Nilsson S.G. 2001. Age and reproduction in lesser spotted woodpeckers (*Dendrocopus minor*). Auk 118: 624–635.
- Williams G.C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am. Nat. 100: 687–690.
- Zanette L. 2001. Indicators of habitat quality and the reproductive output of a forest songbird in small and large fragments. J. Avian Biol. 32: 38–46.

SAMENVATTING

Jonge zangvogels hebben vaak in hun eerste levensjaar een lager broedsucces dan adulte vogels. Dit geldt zeker ook voor de Citroenkanarie *Carduelis [citrinella]*. De auteurs hebben in de naaldbossen van het Zwarte Woud, de Pyreneeën, Corsica en Sardinië de legselgrootte, uitkomstpercentage, broedsucces (percentage eieren dat een uitgevlogen jongen oplevert) en het nestsucces (percentage nesten waarvan ten minste één jong uitvloog) bepaald van subadulte en adulte Citroenkanaries. Bij paren waarvan minstens een van de vogels subadult was, viel het nestsucces lager uit dan bij paren waarvan beide vogels adult waren. Was de subadulte ouder een man, dan was ook het broedsucces lager. Citroenkanaries zijn waarschijnlijk weinig productief gedurende hun eerste broedseizoen omdat de vaardigheden om voedsel te zoeken in de relatief arme naaldbossen nog onvoldoende is ontwikkeld. Zo'n eerste poging zou dus vooral worden gedaan om voldoende kennis te verwerven voor volgende jaren. De Citroenkanarie is een relatief langlevende soort. Vogels van deze soort kunnen zich daarom een lange leerperiode veroorloven. (YIV)

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