The ecological consequences of solitary breeding in a species with bi-parental care

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A higher rate of nestling development reduces their exposure time to predators, which is advantageous but simultaneously it involves an increased parental investment in incubation, brooding and feeding, which may be difficult to obtain by a single parent. An interesting question is whether, and to what degree, a single parent in a typical bi-parental species is able to compensate the lack of its mate's contribution in species with fast developing nestlings. Our study species is the Blackcap *Sylvia atricapilla*, a small passerine that experiences high levels of nest predation and rapid development of nestlings. We test the hypotheses that (i) single parents are not able to fully compensate for the lack of mate in rearing a brood and (ii) parents pay cost for breeding alone by increasing the time that the offspring is exposed to predators in the nest. We also inquire in potential trade-off between brooding and feeding and its consequences for nestling growth in nests reared by single parents. Our results show that single parents were able to compensate for the lack of the mate in terms of feeding rate, but this was at the cost of time spent brooding. Nestlings in uni-parental nests grew more slowly and lagged about two days behind their bi-parental counterparts, which may extend nestling exposure time to a predator by about 20%. In an environment with high nest predation risk, this is expected to strongly affect offspring survival. Slower growth of single-parent nestlings might have resulted from deficiency in brooding of poikilothermic offspring observed in our study, which reveals the important role of both mates in shortening the nestling period. It also demonstrates that although single parents are capable of full mate compensation in one activity, it is by the cost of other parental investments, finally leading to impairment in offspring development.

1. Introduction

The majority of bird species are characterized by bi-parental care of nestlings (reviewed by Cockburn 2006). In several bird species bi-parental care is facultative (Maxson & Oring 1980, Kalas 1986, Webster 1991, Pinxten *et al.* 1993, Reneerkens at al. 2014, Griggio 2015), while in others it is obligatory (Erckmann 1981, Brunton 1988). Parental care adds greatly to the cost of reproduction thus the decision about parental investment should maximize lifetime reproductive success, which is not necessarily the success for a single breeding attempt. Such decisions may create a conflict be-

tween parents, known as sexual conflict (Trivers 1972, Chapman *et al.* 2003, Arnqvist & Rowe 2005), in which males usually gain more from polygyny whereas females profit from polyandry (Bateman 1948, Queller 1997). It seems that the outcome of the sexual conflict depends on whether mates benefit more from cooperation or from execution of their exclusive interests. Unequal share of parental duties may also be caused by the predation on one of pair members, which is not uncommon during breeding attempts. The decrease of parental effort of one mate may result in several strategies of its partner, such as the maintenance of caring activities at the same level, the increase of its own effort, the decrease of its own effort or the abandonment of the nest (Harrison *et al.* 2009). The decision whether to compensate for a decreased effort of a partner may be shaped, among other things, by future mating opportunities (mate compensation seems more likely in short living species) or the ability of lone parent to care for offspring (for example the presence of a brood patch). Theoretical models predict that the optimal response to a decrease of investment by one parent is the increase of the effort of the other (Wright & Cuthill 1989, Whittingham *et al.* 1994). However, Houston and Davies (1985) demonstrated that bi-parental care is an evolutionarily stable strategy when each parent only partially compensates for the reduction of investment by the partner (*partial compensation hypothesis*), as full compensation would lead to exploitation of one parent and the evolution of uni-parental care.

On the other hand, in extreme environments a full contribution of both parents may be needed to ensure breeding success, thus partial compensation of decreased effort of one parent has a detrimental effect on brood survival. For example, avian eggs develop optimally in a narrow range of temperatures (Drent 1975, Webb 1987), therefore very low or hot ambient temperatures require both parents for the effective incubation and brooding, leaving little opportunity for negotiations between mates over parental investments (AlRashidi *et al.* 2010, 2011). Another circumstance that may extort high investment of both mates is the risk of nest predation (Davies 1991, Amat *et al.* 1999, Ligon 1999, Conway & Martin 2000, Bennett & Owens 2002). Higher rate of nestling development shortens their exposure time to predators which is

advantageous, but simultaneously it involves an increased parental investment in incubation, brooding and feeding (Bosque & Bosque 1995, Martin 2002, Martin *et al.* 2011, Hua *et al.* 2014), which may be difficult to obtain by a single parent. An interesting question is whether, and to what degree, a single parent is able to compensate the lack of its mate contribution in case of fast developing nestlings. The inability for such compensation would demonstrate the cost paid by lone parents in the bi-parental species suffering from high nest predation.

Most studies testing the compensatory hypothesis in birds used nestling provisioning as the proxy for variation in parental effort (reviewed in Hinde 2006, Harrison *et al.* 2009). However, given that altricial nestlings are poikilothermic during the first stage of nestling period, brooding constitutes an important component of parental investment. During the period of thermal dependence of nestlings, parents face a trade-off between the need to brood their young and the need to forage for them (Ricklefs 1983, Kaiser *et al.* 1990). Because foraging and brooding cannot be performed simultaneously, time, which is a limited resource, must be allocated between them. According to the Principle of Allocation, extra time channelled to any of parental activities should result in less time available to the remaining ones. Thus testing the compensatory hypothesis in regards to more parental behaviours than just provisioning would provide a wider picture of parental compensatory abilities.

Our study uses the data collected in 6-year field study on the Blackcap *Sylvia atricapilla* – a bi-parental species that experiences high nest predation and rapid development of nestlings (Węgrzyn 2013). Typically both parents participate in nestling brooding and provisioning, as well as nest cleaning from parasites. However during the study we came across some nests cared for by single parents, which provided the unique possibility to test compensatory abilities of lone parents and to compare the effect of uni-parental and bi-parental care on nestling development without the need of harmful experiments involving parental removal, in which removed birds are often sacrificed due to difficulties to keep them alive in cages for many days (i.e., Bjørnstad & Lifjeld 1996 but see Markman *et al.* 1996). Our research policy has always

been to widen the knowledge of animal behaviour in the way as friendly as possible to subjects of our investigations. In the current paper, using data from naturally occurred cases of uni-parental and bi-parental care in Blackcap nests, we test the hypotheses that (i) single parents are not able to fully compensate for the lack of mate in rearing a brood and (ii) parents pay cost for breeding alone by increasing the time that the offspring is exposed to predators in the nest. We also examine the potential trade-off between brooding and feeding and its consequences for nestling growth in nests reared by single parents.

2. Material and methods

2.1. Species and study area

The present investigation is a part of a larger project on the behavioural ecology of the Blackcap conducted over the period 2008–2015. The current study uses data collected in 2009–2014 in the deciduous forest of the Fox Hill Reserve on the outskirts of Rzeszow, south-eastern Poland (50°600"N, 21°59024"E).

The Blackcap is a small, migratory, open-nesting passerine that breeds in Europe. It prefers habitats characterized by dense tree and shrub vegetation (Glutz von Blotzheim & Bauer 1991). It builds thin-walled, open cup nests in the shrub and herbaceous layers of forests (Storch 1998). The clutch size is three to six eggs laid on consecutive days. Incubation lasts about 12 days and nestlings stay in the nest for another 12 days, but they are able to leave the nest when 9 days old. Nestlings are typically fed and brooded by both parents; males develop brood patches similar to that of females (pers. obs., Redfern 2008, 2010). Brooding takes place throughout the nestling period but decreases prior to fledging. All nestlings within a brood fledge at the same time (E. Węgrzyn pers. obs.). The Blackcap suffers from high rates of nest predation, mostly by rodents and corvids (Weidinger 2002). On average only 30% of nests escape predation (nest success reported from different countries: 20% – Germany (Schaefer 2004), 31% – Czech Republic (Weidinger 2000), 42–61% – Slovakia (Baláž *et al.* 2007), 20–49% – Poland (Węgrzyn & Leniowski 2011, Zieliński

2011). Similar nest success (34%) was observed in our study site (Węgrzyn 2013).

2.2. Data collection

Nests were searched by careful inspection of potential nest-sites after mapping male breeding territories in the spring. We searched for nests from mid-April until the end of June in all years of the study to monitor complete breeding success in the studied species. However in the current study we used only the data of first breeding attempts during a season. We chose such approach to avoid confounding factors, like a possible decrease of parental condition during repeated breeding attempts, as well as different food availability, air temperature and day length with the progression of breeding season. Blackcap first breeding attempts are highly synchronous (there is no more than a 4-day difference in the start of egg laying between nests; E. Węgrzyn pers. obs.). We used the nest monitoring protocol described in Węgrzyn (2013). Where possible we checked poorly concealed nests using binoculars to minimize the disturbance to incubating birds. Nest concealment was estimated as a percentage of the nest bowl obscured by foliage. Nest vertical and horizontal concealment were estimated by observing the nest from distances of 1m, vertically above the nest and in the four cardinal directions at the nest level. These five estimates were averaged to obtain a single percentage for a nest (Remeš 2005, Węgrzyn & Leniowski 2011). Estimates were done to the nearest 10%. A 13-cm diameter mirror mounted on a telescopic pole was used to estimate concealment, especially from above, of nests that were sited too high for direct inspection.

Nests with hatchlings aged 3–4 days were filmed for 1 hour between 6.00 a.m. and 9.00 a.m. The following data were later extracted from recordings: (i) feeding rate, (ii) brooding rate and duration, (iii) nest sanitation rate and duration. Durations of parental activities were rounded off to the nearest whole second.

To compare the development of nestlings reared by one and two parents, respectively, we weighed nestlings daily (between 18:00 and 20:00 hours) using an electronic jewellery scale for nestlings aged 1–5 days and a pesola scale for older

Fig. 1. Mean mass (± SE) in relation to nestling age of nestlings reared by two parents (filled circles) and a single parent (open circles). Annotations under circles indicate the number of nestlings that were weighted. Reference lines illustrate that the mean mass of 8-day-old nestlings reared by a single parent matches the mean mass of 6-day-old nestlings reared by two parents.
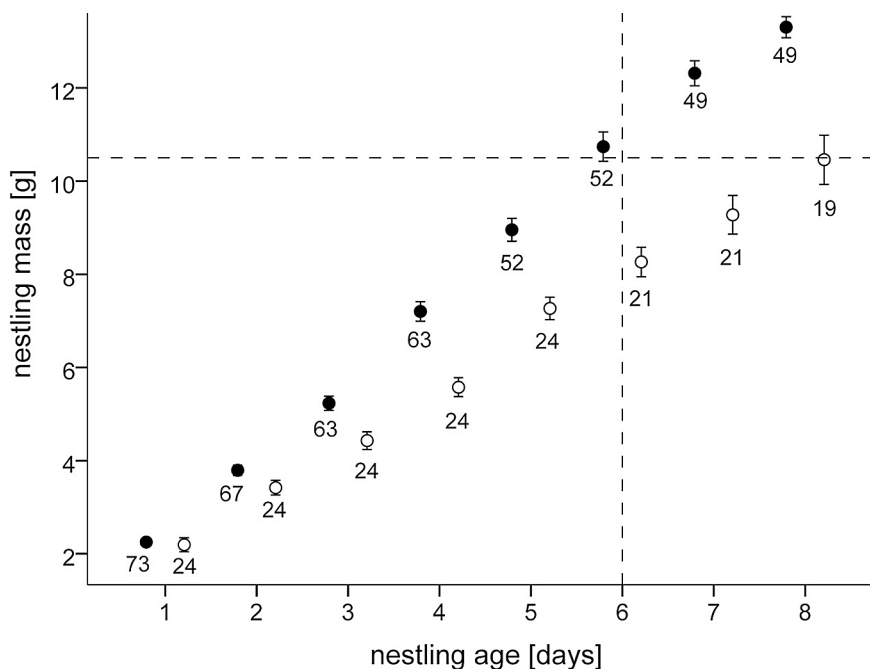
nestlings. The measurements were taken to the nearest 0.1 g. The last measurements were taken when nestlings were 8 days old (hatching = day1) because nestlings may escape from the nest when handled at the age of 9+ days.

2.3. Filming procedure

A micro-camera (of thumb-nail size) was placed about 25 cm from the nest and left for 1 h to allow parents to resume their natural feeding activity. We used the micro-camera (Sony 1/4" CCD matrix, pinhole lens; Tokyo, Japan) connected to a laptop through a Pinnacle Studio 10 USB video converter. For more detailed description of camera mounting refer to Węgrzyn & Leniowski (2015). Male and female identity was recognized based on sexual dimorphism between parents: a male has a black cap while a female brown one, which is easily distinguishable on the recordings.

2.4. Statistical analyses

All analyses were conducted using SPSS 20 software (SPSS Inc., Chicago). Differences in mass between uni-parental and bi-parental nestlings were tested using Linear Mixed Model with nestling as a subject, nestling measurements in subsequent days of life as a repeated measure, nestling mass as a dependent variable, type of parental care (uni-parental vs. bi-parental) and brood size as fixed factors, nest concealment as a covariate and nest ID as a random factor (to control for this variable). Differences in workload (feeding rate, brooding time, sanitation rate, brooding time, and sanitation time) of single parents and couples were analysed using Mann-Whitney Test. Differences in egg masses and brood sizes between single parents and couples were tested using Mann-Whitney Test.

3. Results

3.1. The incidence of bi- and uni-parental care in Blackcaps

During a 6-year study we documented parental investment in Blackcaps in 56 nests containing nestlings. In 50 of them (89.3%) both parents took care of nestlings and in the remaining six nests (10.7%) only one parent reared nestlings. In four cases it was a male and in two cases a female.

Table 1. Comparison of egg masses and brood sizes between single and mated parents.

	Egg mass [g]		Brood size	
No of parents	1	2	1	2
Mean	2.1	2.09	4	4.2
Min	1.86	1.68	3	3
Max	2.56	2.43	5	5
SD	0.17	0.16	0.63	0.73
No. of nests	6	13	6	13
No. of eggs/nestlings	25	58	24	55
Test	Mann-Whitney U = 642, p = 0.85		Mann-Whitney U = 46.5, p = 0.59	

Table 2. Comparison of the workload of single parents (1) vs. couples (2), nestling age: 3–4 days.

	Feeding rate per hour		Brooding rate per hour		Brooding duration [s]		Nest sanitation rate per hour		Nest sanitation duration [s]	
No. of parents	1	2	1	2	1	2	1	2	1	2
Mean	6.8	7.6	2.5	8.7	1,199	2,080	1.8	1.6	89	102
Min	4	2	0	0	0	0	0	0	0	0
Max	12	15	5	13	2,165	3,167	9	9	483	1,106
SD	2.71	3.5	1.76	3.22	696.38	851.8	3.54	2.4	193.6	301.93
No. of nests	6	13	6	13	6	13	6	13	6	13
Difference	Z = −0.268 P = 0.789		Z = −2.956 **P = 0.003**		Z = −2.325 **P = 0.02**		Z = −0.693 P = 0.488		Z = −0.676 P = 0.499	

3.2. Nestling development in nests of bi- vs. uni-parental care

Nestlings reared by both parents grew faster than those reared by a single parent and the difference in mass between bi- and uni-parental broods was significant (LMM: F = 48.560, p < 0.001), irrespective of the brood size and nest concealment, which did not affect nestling mass significantly (LMM: F = 0.913, p = 0.447 and F = 0.008, P = 769, respectively). Also, the difference in mass between the two categories of nestlings increased with nestling age and the weight of eight-day-old single parent nestlings matched the weight of six-day-old nestlings reared by two parents (Fig. 1). This shows a two-day delay in a development of single parent nestlings at the time when nestlings cared by two parents are close to fledge (Blackcap nestlings are able to fledge at the age of 9 days; Węgrzyn 2013).

3.3. Workload of single parents and couples

The investment of single parents was documented in six nests containing 24 nestlings aged 3–4 days. We compared these data to data obtained from 13 nests containing 55 nestlings of the same age reared by two parents. Brood sizes as well as egg masses in uni-parental and bi-parental nests did not differ significantly (Table 1) suggesting similar quality of single parents and couples. Feeding rate did not depend on the number of parents (Table 2) indicating that, at least in nests with young nestlings, single parents were able to compensate for the lack of the other parent. Similarly, nest sanitation was performed at similar level in uni-parental and bi-parental nests (Table 1). However, brooding rate and duration was significantly higher in nests reared by two parents than in single-parent nests (Table 1). This shows that single parents forced to make more frequent feeding trips

are not able to brood their nestlings as effectively as couples, which alternate with each other in feeding and brooding. In fact, brooding rate in uni-parental nests decreased by 71% and brooding duration by 42% in comparison to bi-parental nests.

4. Discussion

Our study demonstrates that Blackcap nestlings reared by two parents develop faster than those reared by a single parent. Interestingly, the slower development of single-parent nestlings might have resulted from reduced time being brooded, at least at the early nestling stage. Blackcap nestlings are poikilothermic until seven days old (Węgrzyn 2013) and during this time the effectiveness of their development may depend both on feeding rate and brooding time provided by parents. Although single parents in our study were able to compensate for the lack of a mate in terms of feeding rate, it was at the cost of time spent brooding. In our study, single parents reduced the time spent brooding by 42%. Similar responses were reported in male-removal experiments on Savannah sparrows *Passerculus sandwichensis* (Weatherhead 1979) and Dark-eyed juncos *Junco hyemalis* (Wolf *et al.* 1988). Interestingly, removal experiments conducted at poikilothermic nestling stages on other bird species also revealed slower growth of single parents nestling (Johnson *et al.* 1992, Markman *et al.* 1996) despite the fact that females were able to compensate completely in terms of feeding (but not brooding) for the loss of male assistance (Bjørnstad & Lifjeld 1995). Such parallel findings in natural and experimental systems demonstrate that in species of bi-parental care, single parents face a conflict between increasing the provisioning and brooding of young. The level of such conflict may depend on the ambient temperature and the availability of food, creating more or less demanding conditions for single parents.

Theoretically, poorer growth of single-parent nestlings may also be explained by lower quality of single parents. We do not know whether uni-parental broods were caused by a predation or a desertion. However, the lack of differences in egg masses and brood sizes between uni-parental and bi-parental nests indicates similar condition of adults, as above features have the potential to re-

flect quality of parent birds (Slagsvold & Lifjeld 1990, Rish & Rohwer 2000, Silva *et al.* 2007, Robinson *et al.* 2014). It should also be noted that we did not control for the prey size delivered by single parents and pairs. Although feeding rate in uni- and bi-parental nests was comparable, there still might have been differences in prey quality and size.

We are not sure whether single parents were still able to feed their young as effectively as couples when nestlings became endothermic because food demands of nestlings increase dramatically with the onset of thermoregulation (Węgrzyn 2013). Unfortunately, we did not have the data to compare feeding rate by single parents and couples in nests containing endothermic young. Some studies suggest that the lack of bi-parental care is more detrimental in the first few days after hatching than later on (Bart & Tornes 1989, Johnson *et al.* 1992). Yet, the difference in mass between the two categories of nestlings in our study increased with nestling age (Fig. 1), suggesting that single parents may have delivered less food than couples to older nestlings. It seems quite likely that nestlings of single parents experienced deficient brooding at poikilothermic stage and deficient feeding at endothermic stage when food demands are particularly high.

Studies investigating the effect of uni-parental and bi-parental care on nestling development in natural circumstances are scarce because in species of typical bi-parental care the cases of a single parent brood occur relatively rarely. This makes such investigations time consuming and risky (as one may not find a sufficient sample size). An example of such a study, conducted on Iberian Rock Sparrow *Petronia petronia* (García-Navas *et al.* 2013), demonstrated a poorer development of nestlings cared for by single parents compared to nestlings of two parents, which concurs with the findings of our study. Interestingly, both studies conducted in natural systems found males and females as single parents, demonstrating that despite the negative effect of uni-parental care on nestling growth each sex is able to raise a brood. In contrast, all experimental approaches investigated solely the effect of male removal on offspring development and survival (reviewed in Møller 2000), leaving the question of single fathers unanswered. In all species in which males significantly

participated in brood rearing, their removal negatively affected nestlings (reviewed in Bart & Tornes 1989, Mřller 2000) as females were not able to compensate completely for the loss of male assistance (Leffelaar & Robertson 1986, Wright & Cuthill 1989, 1990a, b, Hatchwell & Davies 1990, Wolf *et al.* 1990). Thus, it seems that experimental studies have not derived any different outcomes than our observational study, except for the fact that they were restricted to single mothers as care givers and were often conducted in a less ethical way involving scarification of male parents. Notably, the sample size of uni-parental nests in experimental studies varied between six and ten (i.e., Johnson *et al.* 1992, Bjørnstad & Lifjeld 1995, Markman *et al.* 1996), which is not considerably higher than sample size of our observational study ($n = 6$) or a similar study by García-Navas (2013, $n = 6$). Thus our results should be considered as representative for this kind of investigation, where a higher sample size is either unlikely to be obtained in natural systems or unethical in terms of experimental approach.

The most important result of our study demonstrates that bi-parental care speeds up offspring development by two days, which may shorten the time nestlings spend in the nest by about 20%. A similar effect was found by Bjørnstad & Lifjeld (1995) in removal experiments on the Willow warbler, a species experiencing comparable levels of nest predation to the Blackcap (Tiainen 1983). In habitats with high nest predation risk, assuring a high growth rate of nestlings is expected to strongly increase offspring survival. The rate of Blackcap nest predation in our study was high and typically less than 30% of nests produced fledglings (Węgrzyn 2013, Węgrzyn & Leniowski 2015). The species would benefit from fast nestling development resulting in the ability of early fledging since mobile fledglings have greater chance of escaping predators. Our study reveals the important role of both mates in increasing the pace of nestling growth, which in turn may explain the need of bi-parental care in species suffering from heavy nest predation.

Yksinhuoltajaemon vs kahden vanhemman pesintämenestys: kustannukset poikasten kehitykselle?

Poikasten nopea kehitys ja kasvu vähentää aikaa, jolloin ne ovat alttiina saalistukselle. Toisaalta tämä lisää panostusta hautoma-aikana, poikasten lämmittämiseen ja ruokintaan, mikä voi olla vaikeaa kun vain yksi emolintu huolehtii poikasista. On epäselvää, kuinka paljon yksinhuoltajaemo voi kompensoida partnerin vanhempainpanostusta nopeakasvuisilla lajeilla, joilla normaalisti molemmat emolinnut hoitavat poikasia. Mustapääkerttu on pienikokoinen, erittäin nopeakasvuinen varpuslintu, jolla on korkea pesäpredaatioriski. Testasimme mustapääkertulla seuraavia hypoteeseja (i) yksinhuoltajaemo ei pysty täysin kompensoimaan partnerin vanhempainpanostusta (ii) yksinhuoltajaemon poikaset ovat alttiina pesäpredaatiolle pidempään.

Tutkimme myös resurssien allokaatiota poikasten lämmittämiseen ja ruokintaan, ja näiden kustannuksia poikasten kasvuun ja kehitykseen. Havaitsimme, että yksinhuoltajaemot pystyivät kompensoimaan partnerin puuttumisen ruokintafrekvenssien määrässä, mutta tämä johti siihen, että emot käyttivät vähemmän aikaa poikasten lämmittämiseen.

Yksinhuoltajaemojen poikaset kasvoivat hitaammin, ja niiden kehitys oli noin kaksi päivää jäljessä normaaliin verrattuna. Hidas kasvu voi johtua siitä että emo ei lämmittänyt poikasia riittävästi. Hidas kasvu pidensi aikaa, jolloin poikaset olivat alttiina saalistukselle noin 20 %. Ympäristössä, jossa on korkea saalistusriski, tämä todennäköisesti vaikuttaa huomattavasti poikasten eloonjäävyyteen. Yksinhuoltajaemot siis pystyivät kompensoimaan partnerin puuttumisen osassa, mutta ei kaikissa vanhempainpanostuksissaan, mikä johti poikasten kehityksen viivästymiseen.

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