Animal Behaviour 105 (2015) 63–78

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Commentary

Immediate effects of capture on nest visits of breeding blue tits, *Cyanistes caeruleus*, are substantial

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ARTICLE INFO

Article history:
Received 17 October 2014
Initial acceptance 16 December 2014
Final acceptance 2 April 2015
Available online 16 May 2015
MS. number: 14-00837R

Keywords:
blue tit
capture
Cyanistes caeruleus
feeding
handling
human disturbance
nest visit
parental care
trapping

Although capture, handling and marking of birds as well as taking samples from them are ubiquitous and, in most cases, unavoidable procedures in ornithological research, their immediate effects on the individuals remain largely unstudied. Here, we present data over 3 years from a long-term field study on the breeding biology of the blue tit. Parents were captured at the nest when feeding 9–11-day-old young. For all birds, we measured the time of their first visit to the nest after capture and could thus establish their latency of return to the nest. After capture, parents stayed away a surprisingly long time (average 4.2 h, up to 18 h) and nests were not visited by either parent for a duration that almost never occurred under natural conditions. Parental return latencies were strongly associated with previous captures. Birds caught, marked and sampled previously returned on average 4.4 h earlier than new birds. Still these birds took on average 1.9 h to return. Thus, capture itself can have strong effects on immediate behaviour. Once the birds returned to the nest, the time between nest visits was similar to that observed before capture, indicating that birds resumed normal feeding activities. Return latencies of parents and the time nests were left alone had no long-term effects on offspring or breeding success. We discuss possible causes of delayed parental return and methodological implications.

Identifying, tracking, conducting behavioural assays or collecting samples from individuals is an integral part of almost every study of the behaviour of wild animals (Boitani & Fuller, 2000; Bookhout, 1994; Krebs, 1999). Inevitably, then, individuals undergo a protocol of capture, handling, marking and often sampling (CHMS) which may significantly affect them or their offspring. This is especially true in studies of breeding birds, because these usually aim to identify parents and therefore adults are caught in or close to the nest (Kania, 1992).

Two avenues of ornithological research have assessed effects of CHMS on the individual. First, many studies have examined long-term fitness consequences of CHMS, i.e. changes in (1) reproduction (breeding cycle, territory residency, nest desertion, brood size, fledging success, reproductive success), (2) survival (mortality, recruitment, return, recapture and resighting rates), (3) condition (deterioration, injuries, body mass changes, energetic expenditure) or (4) behaviour (impairment of flight, swimming, migration, foraging, display, dominance, mating, communication, recognition) (Calvo & Furness, 1992; Duarte, 2013; Fair, Paul, & Jones, 2010; Griesser et al., 2012; Murray & Fuller, 2000; Owen, 2011; Spotswood et al., 2012). These studies typically aim to understand whether and to what extent specific CHMS procedures (trapping, marking, tagging, sampling) may permanently affect individuals, impact negatively on the study population or bias measurements relevant to the study.

A second line of research has examined immediate physiological effects of CHMS (Duarte, 2013, chapters 2–4), in particular hormonal changes (Romero, 2004; Van Hout, Eens, Darras, & Pinxten, 2010; Wingfield, Vleck, & Moore, 1992). Indeed, the ‘capture–handling–restraint’ method has become a standard technique to study avian stress responses in the wild (Lynn & Porter, 2007). These studies show that CHMS causes a substantial stress response (e.g. Canoine, Hayden, Rowe, & Goymann, 2002; Romero & Reed, 2005; Romero & Romero, 2002; Wingfield et al., 1992), triggering a diversity of changes relevant to bird health and behaviour (e.g. Culik, Adelung, & Woakes, 1990; Duarte, 2013, chapter 4; Matson, Tieleman, & Klasing, 2006; Van Hout et al., 2010).

Given these results, as well as easily observable distress behaviour during CHMS (e.g. Duarte, 2013, chapter 2; Laiolo, Banda, Lemus, Aguirre, & Blanco, 2009), most researchers are well aware

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http://dx.doi.org/10.1016/j.anbehav.2015.04.010

that birds perceive CHMS as a stressful event (Duarte, 2013; Fair et al., 2010), but in general regard them as being able to cope well with CHMS and recover quickly, returning to normal behaviour (Calvo & Furness, 1992). However, studies verifying this assumption by examining immediate effects of capture on behaviour are limited both in number and by the sample sizes on which they are based (Angelier, Weimerskirch, & Chastel, 2010; Ardern, McLean, & Anderson, 1994; Duarte, 2013, chapters 3, 5; Goymann & Wingfield, 2004; MacLeod & Gosler, 2006; Nisbet, 1981). Most reports on short-term behavioural changes after CHMS remain anecdotal (Calvo & Furness, 1992). In addition, few studies have considered consequences of capture per se on individuals, because capture is almost always combined with additional handling procedures, which alter the intactness of the bird's body (marking, tagging, sampling).

Recent advances in passive integrated transponder (PIT) technology make it possible to record behaviour of caught individuals automatically, without disturbance (Bonter & Bridge, 2011). Here, we used this method to investigate how long blue tits caught at the nest when feeding young take to return to the nest after CHMS. We thus inspected the combined consequences of capture, handling, marking and sampling on the behaviour of parents. The CHMS methods implemented in our study are standard procedures in studies of avian breeding biology (Fair et al., 2010) and understanding their consequences is important for planning studies and evaluating data. A second aim of our study was to examine whether variation in return latencies reflects biologically relevant information in terms of individual repeatability, condition, mating status or parental investment.

METHODS

We studied a population of blue tits near Landsberg am Lech, southern Germany (‘Westerholz’, 48°08′26′N, 10°53′29′E) in 2010–2012. This analysis is part of a long-term study monitoring bird activity at nestboxes via registration of birds with transponders passing through the nest hole. Boxes are permanently equipped with reading devices installed in the front panels, invisible to the birds. Details and ethical implications are described in Schlicht, Girg, Loës, Valcu, and Kempenaers (2012). Permits were obtained from the Bavarian government and the Bavarian regional office for forestry (LWF).

Field Procedures

For the captures that are the focus of this study, adult birds were caught in the nestboxes when feeding chicks on day 9, 10 or 11 after the first young had hatched by blocking the entrance hole. Capture time was noted while passing a transponder through the nest hole, allowing a synchronization of the logger's clock with an external watch. Birds were carried in a bird bag to a nearby (ca. 100–1000 m away) parked van, where they were handled. After handling, birds were brought back to their territory and released, with release time noted. Retention time was the duration between capture and release. Previous experience with this species suggests that nest desertion after capture increases for captures late in the day. For this reason, birds were never caught after 1500 hours (except in two cases).

All birds were measured (tarsus, third distal primary), weighed, sexed and aged following Svensson (1992) as yearling or older. For birds that had already been caught on a previous occasion (known birds, $N = 106$ in our sample), this completed the treatment protocol. Birds that were unknown (new birds, $N = 80$ in our sample) had a blood sample taken (4–10 μl, maximum 15 μl; from the brachial vein) and received a metal ring, three coloured plastic rings and a small PIT tag (EM4102 ISO animal tag 134.2 kHz ISO, 8.5 mm × 2.12 mm, 0.067 g), which we inserted under the skin of the back (Nicolaus, Bouwman, & Dingemanse, 2008). Birds not caught before, but hatched on the study site (recruits, $N = 98$ in our sample), were treated like new birds, but did not receive a metal ring. If a transponder had been attached at the nestling stage, the recruit was not tagged again. In addition to this baseline protocol, further data were collected in each year. In 2010, we took feather samples (snippets of four upperwing coverts and one proximal rectrix) from recruits and new birds and a preen gland wax sample from all birds (Soini et al. 2007). In 2011, all except nine birds performed a behavioural test (Mutzel et al., 2013). In 2011 and 2012, sperm samples were taken from 16 and eight males, respectively (Schmoll & Kleven, 2011). We use the variable ‘capture status’ to distinguish between known birds, local recruits and new birds. It is used in a purely descriptive sense and not as a reflection of the corresponding procedures. Note that the 98 recruits received different treatments between years, because in 2010 ($N = 22$ of 22) and 2011 ($N = 16$ of 17) recruits had already received a PIT tag as nestlings, but not in 2012 ($N = 1$ of 59). Effects of treatments that were not part of the baseline protocol cannot be separated from annual variation. Our data set includes seven secondary females of socially polygynous males. There was no difference in return latency, partial brood mortality or brood failure and results remained almost identical when they were excluded.

Transponder Data

Return time was established as the first reading of a bird's transponder number after its release on the territory. Parental return latency was calculated as the time between release and return of a captured bird. In addition, we defined the duration of parental absence at the nest as the time between capture of the last caught parent and the first return of a parent. Return latencies and absence durations are thus the measures of interest for the following analyses.

During the chick-feeding period, parents alternate foraging trips with visits to the nests. This results in natural periods of parental absence between visits. For a comparison with the absence durations following capture, we inspected these time gaps between visits for days 7–16 posthatch (when both parents feed and nestlings are not yet in fledging condition), excluding days of capture and ringing of nestlings as well as overnight gaps. We extracted time intervals between two consecutive readings of transponders. Gaps smaller than 2 min were excluded, because they often represent readings related to the same visit.

Some birds ($N = 39$) returned only on the day following capture. For this reason the duration of the night was subtracted from all return latencies and this is used as adjusted return latency in the following (giving adjusted absence durations). Duration of the night was calculated based on the mean duration of natural overnight gaps (mean ± SE: 8.9 ± 0.001 h; range 7.9–11.0 h; $N = 618$). Note that adjustment using the minimum or maximum duration instead of the mean duration led to almost identical results.

Variables and Tests

We tested the association of return latencies and capture-induced absence durations with three different types of explanatory variables: (1) type A variables are characteristic of the focal individual, i.e. sex, age, morphometrics (tarsus, third distal primary, weight, condition), previous breeding experience (yes/no); (2) type B variables are characteristic of the brood, i.e. brood size (number of young at capture), laying date (date of first egg; excluded in favour of brood size, see Appendix 1), presence of extrapair young (yes/

no), brood morphometrics (average brood tarsus, weight and condition); (3) type C variables are linked to the handling of birds, i.e. capture status (known bird, recruit, new bird), retention time, capture date, capture time, first or second caught bird at a nest.

Note that recruits PIT-tagged as chicks were not further separated from recruits PIT-tagged at capture, because the distinction coincides with annual variation. Instead, year was included as an explanatory variable in a purely descriptive sense.

Brood and adult condition were calculated as the ratio of weight over tarsus (see Appendix 2). We were able to test for effects of age and previous breeding experience in conjunction with capture status, because known birds include those caught in their first winter (20%).

We also tested whether return latencies or absence durations had an effect on fitness via breeding success (proportion of young fledged, duration of the nestling period, probability of brood failure or partial brood mortality and brood morphometrics). Note that our data set does not include failed nests, at which no parental visit was logged after capture (the absence of data could also be due to technical error). However, nest desertion following capture is rare in the population (see also below). Effects of return latencies and of absence duration on these parameters were almost identical and therefore only results for parental absence duration are shown. Brood morphometrics are used both as explanatory and response variables in association with return latency/absence duration, because young were measured after adult capture (and may therefore be affected by parental return latencies), but may also be representative of the situation of the brood before capture (and hence influence parental decisions about when to return to the nest).

CHMS may also affect the parents' nest visit behaviour after their first return to the nestbox, for example if parents adjust their level of investment to changes in brood need after their absence or to changes in their own state resulting from CHMS. Therefore, we also investigated effects of capture on the duration of naturally occurring gaps between visits in two ways, based on data from 55 nests (2010: 16; 2011: 22; 2012: 17) where ‘ins’ and ‘outs’ could be unequivocally assigned (based on light barrier data). First, on the day of capture, we compared gap durations for visits before capture with those of visits after both captured parents returned to the nest. Second, we compared gap durations after return of both parents on the day of capture with gap durations in the corresponding time period of the day preceding capture (excluding $N = 13$ cases where on that day the other parent had been caught). In addition, we used seven nests from 2012, for which visit rates were already available for both parents before capture (because both parents already carried a transponder). For the visit rates of these nests, we performed the same two comparisons.

Statistical Analyses

Statistical analyses were performed with R 2.15.2 (R Development Core Team, 2011). We used linear mixed-effects models (LMEs; Gaussian error structure; package ‘MCMCglmm’; Hadfield, 2010) with individual identity and nest identity as random variables. There were significant differences in return latencies/absence durations between years (see below). Therefore, the 3 years were initially analysed separately. Because the main results were similar in each year, data were pooled for a common analysis, taking year differences into account via inclusion as a fixed factor (see also above). Frequency distributions of return latencies and absence durations were left-skewed. They were therefore log-transformed when used as response variables to conform to assumptions of normality and homoscedasdicity (Fig. 1). Continuous explanatory variables were centred at their respective mean. *P* values and estimates were obtained by Markov chain Monte Carlo simulations (packages ‘MCMCglmm’; ‘languageR’: 100000 iterations; Baayen, 2010). Credibility intervals are highest posterior density intervals, from which the *P* values are calculated. For models with a binomial error structure, 95% confidence intervals (CI) were calculated by inference from the general linear hypothesis of the model (package ‘multcomp’; Hothorn, Bretz, & Westfall, 2008). For analysis of naturally occurring gaps between visits we used generalized linear mixed-effect models (GLMMs) with Poisson error structure (log link function; package ‘lme4’; Bates, Maechler, & Bolker, 2011). Effects of return latencies on the proportion of young fledged or the probability of brood failure were modelled using GLMMs with binomial error structure (logit link function; package ‘lme4’). We report either estimates followed in parentheses by their 95% CIs or mean values ± SEs.

Effects of variable types A–C on return latencies and absence durations were inspected in two ways. First, explanatory variables were grouped as described above (A–C). For each group separate models were run and variables with large or significant effects were retained. The retained variables from all three groups were then combined in one model (Model 1; see Results), which was further reduced by stepwise exclusion of nonsignificant variables (Model 2). Second, all explanatory variables were combined in one model (Model 3), followed again by stepwise exclusion of nonsignificant terms until only significant terms remained (Model 4). Effect sizes and significances obtained during these procedures were very similar. The resultant Models 2 and 4 were identical (see Appendix 3).

We calculated repeatability of adjusted return latencies (log-transformed) for individuals present in the data set for more than 1 year ($N = 27$; 2010 and 2011: 8; 2010 and 2012: 4; 2011 and 2012: 13; 2010, 2011 and 2012: 2) using the package ‘rptR’ (Schielzeth & Nakagawa, 2011; method ‘REML’, number of bootstrapping runs for asymptotic calculation of 95% CIs:1000; number of permutations for asymptotic calculation of *P* values: 1000). We calculated both agreement repeatabilities and repeatabilities adjusted for capture status (Nakagawa & Schielzeth, 2010), because capture status significantly affected return latencies (see below). Adjusted repeatabilities were obtained by mean-centring log-transformed adjusted return latencies for each capture status.

RESULTS

Descriptive Results

We analysed return data from 284 capture events of 255 individual birds. The proportion of known birds varied significantly between years (Appendix 3, Table A1). Birds were released on their territories on average 30 min after capture (Table 1). Retention times differed between study years, as expected from the changes in the protocol between years (preen gland wax sampling, behavioural test). Retention times were significantly shorter for known birds than for recruits and new birds (Appendix 3, Table A2).

Return latencies varied considerably, ranging from 20 min to 18 h when a bird did not return on the same day (night excluded, see Methods), with an average of 4.2 h (Table 1). Most birds (54%) took more than 2.5 h to return to their nest. This resulted in an average period of 2.9 h where both parents were absent from the nest (range 20 min to 14 h; when parents did not return on the same day, night excluded). In all models, adjusted return latencies and absence durations varied significantly between years, which was not solely a consequence of variation in protocol, but also related to annual differences in the proportion of known birds (Appendix 3, Table A2).

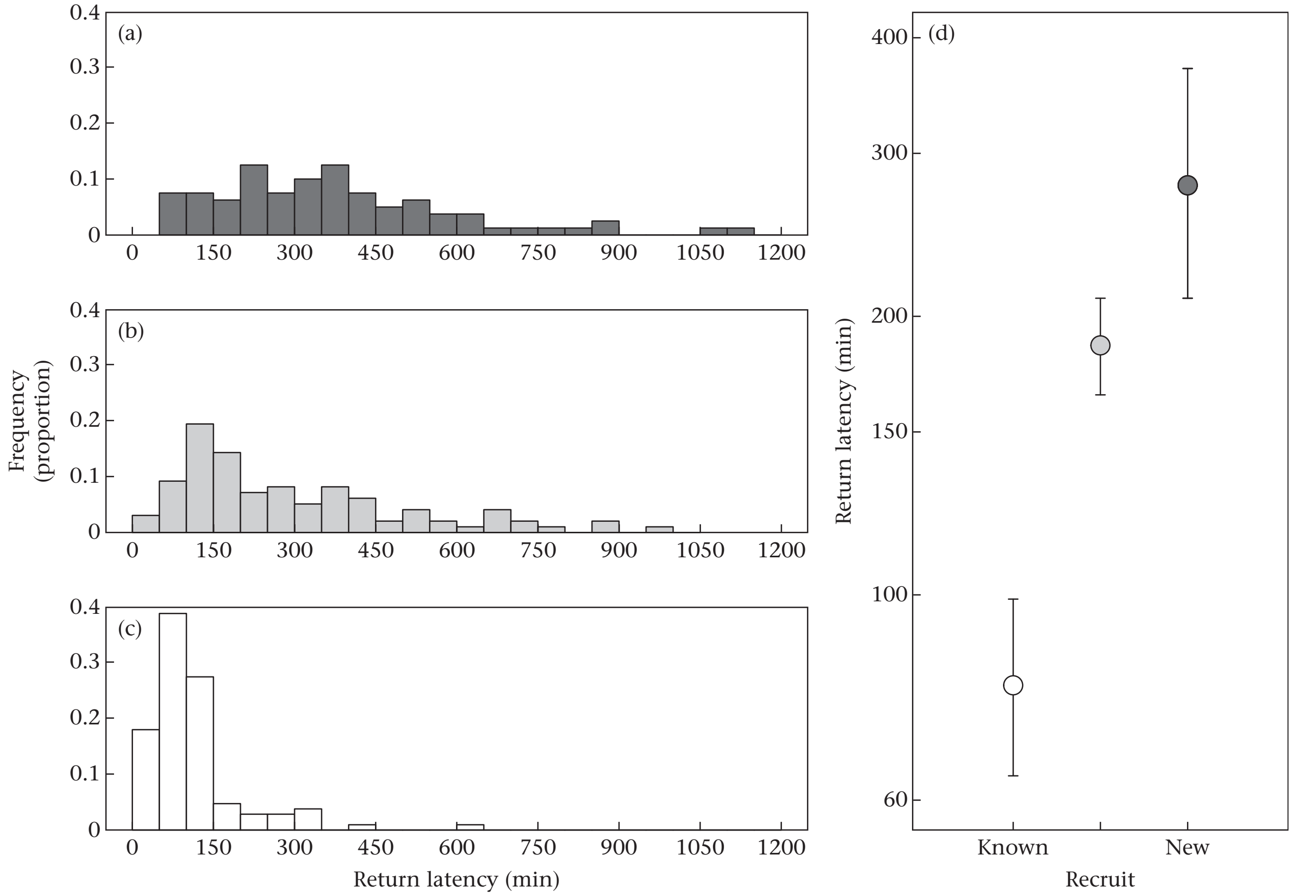

Figure 1. Influence of capture status on return latencies (in min, nights removed). (a)–(c) Data distribution (histogram of relative frequencies, area within bars sums to one). (a) New birds ($N = 80$), (b) local recruits ($N = 98$) and (c) previously caught birds ($N = 106$). (d) Model estimates (model 1) and their 95% confidence region; note the log-scale on the x-axis.

To assess the importance of CHMS in causing long return latencies, we inspected parental return latencies after performing a nest check (chick age at least 8 days, data from 2012). Based on 219 nest checks from 57 nests, the last visit of a focal parent had occurred on average 6.6 ± 0.5 min (range 1 s – 1.1 h) before the nest was checked and the next visit of that parent occurred on average 9.0 ± 0.5 min (range 15 s – 1.9 h) after the nest check.

Explaining Variation in Return Latencies

There was no relationship between the return latencies of the male and female tending the same nest (when controlling for male and female capture status; effect of male on female return latency: negligible, $P(\text{MCMC}) = 0.4$; effect of female on male return latency: increase of male latency by 2 min when female latency is increased

Table 1

Summary statistics for retention time, adjusted return latency[1] and adjusted absence duration[2], for blue tits caught in Westerholz

Variable	Year	Mean±SE	Minimum	Maximum
Retention time[3] (min)	2010	33±2	7	72
	2011	38±2	11	84
	2012	22±1	7	79
	Total	29±1	7	84
Adjusted return latency[1,4] (min)	2010	231±25	29	1102
	2011	173±20	29	1058
	2012	310±19	20	997
	Total	251±13	20	1102
Adjusted absence duration[2,5] (min)	2010	163±20	29	862
	2011	105±10	25	690
	2012	217±14	20	874
	Total	171±14	20	874

[1] Return latencies after capture, adjusted to exclude duration of night for birds returning on the next day (see Methods).
[2] Duration that the nestbox was not attended by any parent; adjusted to exclude duration of night for intervals covering the next day (see Methods).
[3] Annual differences: all $P < 0.001$; see Table A2.
[4] Annual differences: all $P < 0.05$; see also Table A2.
[5] Annual differences: all $P < 0.01$; see also Table A2.

by 1 h, P(MCMC) = 0.06). None of the variables associated with the focal individual (A) or brood (B) were linked to return latencies (Appendix 3, Table A3). Of the variables linked to the handling of birds (C), only the capture status of the focal bird had an effect: on average, known birds returned only after 1.9 h, but 4.4 h earlier than new birds and 3.1 h earlier than recruits (Table 2, Fig. 1; effects of capture date and retention time in the full model became nonsignificant after model simplification: Appendix 3, Tables A3, A4).

Explaining Variation in Absence Durations

Absence durations at the nest were again not linked to individual variables (A) of either parent (Table 3, Appendix 3, Table A5). The analysis of brood variables (B) indicated that larger broods were left alone for longer (Fig. A1a). Adding one nestling to an average brood increased absence duration by 8 (3–13) min (Table 3). Notably, broods with young in good condition were left alone for longer (Fig. A1b). An average increase in nestling condition of 0.1 g/mm increased absence duration by 38 (11–70) min (assuming an average brood size; Table 3). Variables related to handling (C) were again of highest influence (Table 3, Appendix 3, Table A6). First, absence durations increased with capture time (Fig. A1c): delaying capture time from the average to 1 h later in the day increased absence duration by 9 (5–14) min (Table 3). Most importantly, the capture status of both parents combined influenced absence durations (Table 3, Fig. 2). When both parents were new birds, absence durations were on average 7 h (446 ± 46 min, $N = 15$); this dropped to 5 h when at least one parent was a recruit (but neither was known): 317 ± 21 min, $N = 53$. As soon as one of the parents was known, absence durations were considerably shorter (89 ± 6 min, $N = 74$), because the known parent returned earlier, in line with the finding that capture status had the strongest effect on return latencies of single individuals. However, even in broods with both parents known, nests were left alone almost 1.5 h on average (79 ± 5 min, $N = 34$).

Comparison with Natural Absences

Naturally occurring gaps between visits were generally short (4.5 ± 0.02 min; range 2 min to 9.5 h; $N = 81\,435$; days of capture and processing of nestlings excluded; Fig. 3, Appendix 3, Fig. A2), including for the days of capture (4.5 ± 0.09 min; range 2 min to 2.1 h; $N = 3270$). On the day of capture, natural gaps were 10% (6–14%) longer after capture than before (difference in means: 0.3 ± 0.05 min; $N_{\text{after}} = 1852$; $N_{\text{before}} = 1418$; Appendix 3, Table A7). This effect was probably due to an increase in duration of parental absence for the last few nest visits in the evening. Indeed, the difference in gap duration before and after capture was no longer present when the last 10 gaps of the capture day were excluded from the data set (Appendix 3, Table A7). In addition, when comparing the corresponding time intervals of the day preceding capture, the effect was present too (12% (7–16%); difference: 0.6 ± 0.07 min; $N_{\text{after}} = 1721$; $N_{\text{before}} = 1434$; Table A7). Gaps between visits were 6% (3 to 10%) shorter after capture than in the corresponding time interval of the preceding day (difference: 0.3 ± 0.01 min; Table A7).

The comparison of feeding rates for seven nests for which parental visit data were available before capture also showed no differences in the visit rates, either between the time intervals before capture and after return on the capture day or between the time intervals after return on the capture day and the corresponding time intervals of the previous day (all $P > 0.7$).

Effects of Parental Absence

Despite large variation in total absence duration at the box, this variable did not influence the duration of the nestling period, brood morphometrics, brood condition, fledging success or the probability of brood failure (all effect sizes negligible, all P values >0.2; Table 4). Between capture of the parents and the next nest check (performed 3, 4 or 5 days later for 78% of nests; range 1–10 days) 12 broods failed (two nests checked 2 days later; 10 nests 5 days later).

Repeatability of Absence Duration

Repeatability of return latencies was not significantly different from zero ($r = 0.10 \pm 0.13$; 95% CI 0–0.42; $P_{\text{asymptotic}} = 0.28$), even after adjusting for capture status ($r = 0.04 \pm 0.13$; 95% CI 0–0.42; $P_{\text{asymptotic}} = 0.43$).

DISCUSSION

We inspected effects of treatments (CHMS procedures) ubiquitously applied in ornithological field studies (Bonter & Bridge, 2011;

Table 2
Results of a model explaining variation in return latencies of blue tits after capture

Variable		Estimate (95% CI)	Back-transformed estimate[1] (95% CI)	P (MCMC)
	(Intercept)	4.38 (4.15 to 4.59)	79.85 (63.74 to 98.95)	(<0.001)
	Year 2011 versus 2010	+0.15 (−0.15 to 0.46)	×1.17 (0.86 to 1.59)	0.33
	Year 2012 versus 2010	+0.39 (0.17 to 0.64)	×1.48 (1.18 to 1.90)	<0.001
B[2]	Brood size	+0.00 (−0.05 to 0.06)	×1.00 (0.95 to 1.06)	0.91
	Mean tarsus length of chick in brood (mm)	−0.11 (−0.35 to 0.08)	×0.90 (0.70 to 1.09)	0.32
	Mean condition of chick in brood (weight in g/tarsus in mm)	+2.26 (−0.08 to 4.74)	×9.62 (0.92 to 114.76)	0.07
C[2]	Capture date (days)	+0.04 (0.00 to 0.08)	×1.04 (1.00 to 1.08)	0.07
	Capture time (h)	+0.05 (−0.01 to 0.1)	×1.05 (0.99 to 1.11)	0.09
	Capture order (second versus first caught bird at nest)	−0.1 (−0.26 to 0.04)	×0.91 (0.77 to 1.04)	0.21
	Retention time (min)	+0.01 (0.00 to 0.01)	×1.01 (1.00 to 1.01)	0.07
	Capture status[3] (recruit versus known)	+0.32 (0.11 to 0.52)	×2.26 (1.87 to 2.73)	<0.001
	Capture status (new versus known)	+1.15 (0.93 to 1.36)	×3.12 (2.54 to 3.90)	<0.001
	Capture status (recruit versus known)[4]	*+0.34 (0.14 to 0.53)*	*×1.34 (1.15 to 1.70)*	*0.002*

The table shows the results of a linear mixed-effects model (LME) for adjusted return latencies (combined model, Model 1). Response variable is the latency of return to the nest of individual parents in min (night excluded; log-transformed). Identity of focal individuals and brood identity were included as random variables.

[1] After back-transformation from log-scale, the effect is indicated by a factor (×1 indicates no difference).

[2] Explanatory variables linked to the brood (B) or to handling (C, see Methods).

[3] ‘Capture status’ refers to the previous capture and handling experience of the bird (‘known’ = bird known from previous captures, ‘recruit’ = local recruit, ‘new’ = new bird).

[4] The comparison between capture status ‘new’ and ‘recruit’ is shown in italics, because it was extracted from a model in which the variable ‘capture status’ was recoded to include this comparison (i.e. different intercept).

Table 3
Results of a model explaining variation in absence durations of blue tits after capture

Variable		Estimate (95% CI)	Back-transformed estimate[1] (95% CI)	*P* (MCMC)
	(Intercept)	4.22 (4.05 to 4.37)	67.87 (57.37 to 79.20)	(<0.001)
	Year 2011 versus 2010	−0.10 (−0.32 to 0.17)	×0.91 (0.72 to 1.19)	0.43
	Year 2012 versus 2010	+0.35 (0.24 to 0.47)	×1.43 (1.27 to 1.60)	<0.001
B[2]	Brood size	+0.05 (0.02 to 0.08)	×1.05 (1.02 to 1.08)	0.01
	Mean tarsus length of chick in brood (mm)	−0.04 (−0.19 to 0.10)	×0.96 (0.83 to 1.11)	0.55
	Mean condition of chick in brood (weight in g/tarsus in mm)	+2.17 (0.72 to 3.70)	×8.80 (2.05 to 40.50)	0.004
C[2]	Capture date (days)	+0.01 (−0.01 to 0.03)	×1.01 (0.99 to 1.03)	0.39
	Capture time (hour of day)	+0.06 (0.03 to 0.08)	×1.06 (1.03 to 1.09)	<0.001
	Pair capture status[3] (1 versus 0)	+0.77 (0.66 to 0.90)	×2.16 (1.94 to 2.45)	<0.001
	Pair capture status (2 versus 0)	+1.63 (1.47 to 1.83)	×5.08 (4.33 to 6.26)	<0.001
	Pair capture status (2 versus 1)[4]	*+0.86 (0.66 to 1.04)*	*×2.36 (1.93 to 2.84)*	*<0.001*

The table shows the results of a model (LME) for adjusted absence duration (combined model, Model 1). Response variable is the total absence duration of both parents at the nest in min (night excluded; log-transformed). Identity of focal individuals and brood identity were included as random variables.

[1] After back-transformation from log-scale, the effect is indicated by a factor (×1 indicates no difference).

[2] Explanatory variables linked to the brood (B) or to handling (C, see Methods).

[3] ‘Pair capture status’ refers to the joint capture and handling experience of the pair (status 0: at least one of the birds was known from previous captures; status 1: neither of the birds was known, but at least one was a recruit; status 2: both birds were new).

[4] The comparison between pair capture status 2 (both new) and 1 (none known, one or both recruit) is shown in italics, because it was extracted from a model in which the variable ‘capture status’ was recoded to include this comparison (i.e. different intercept).

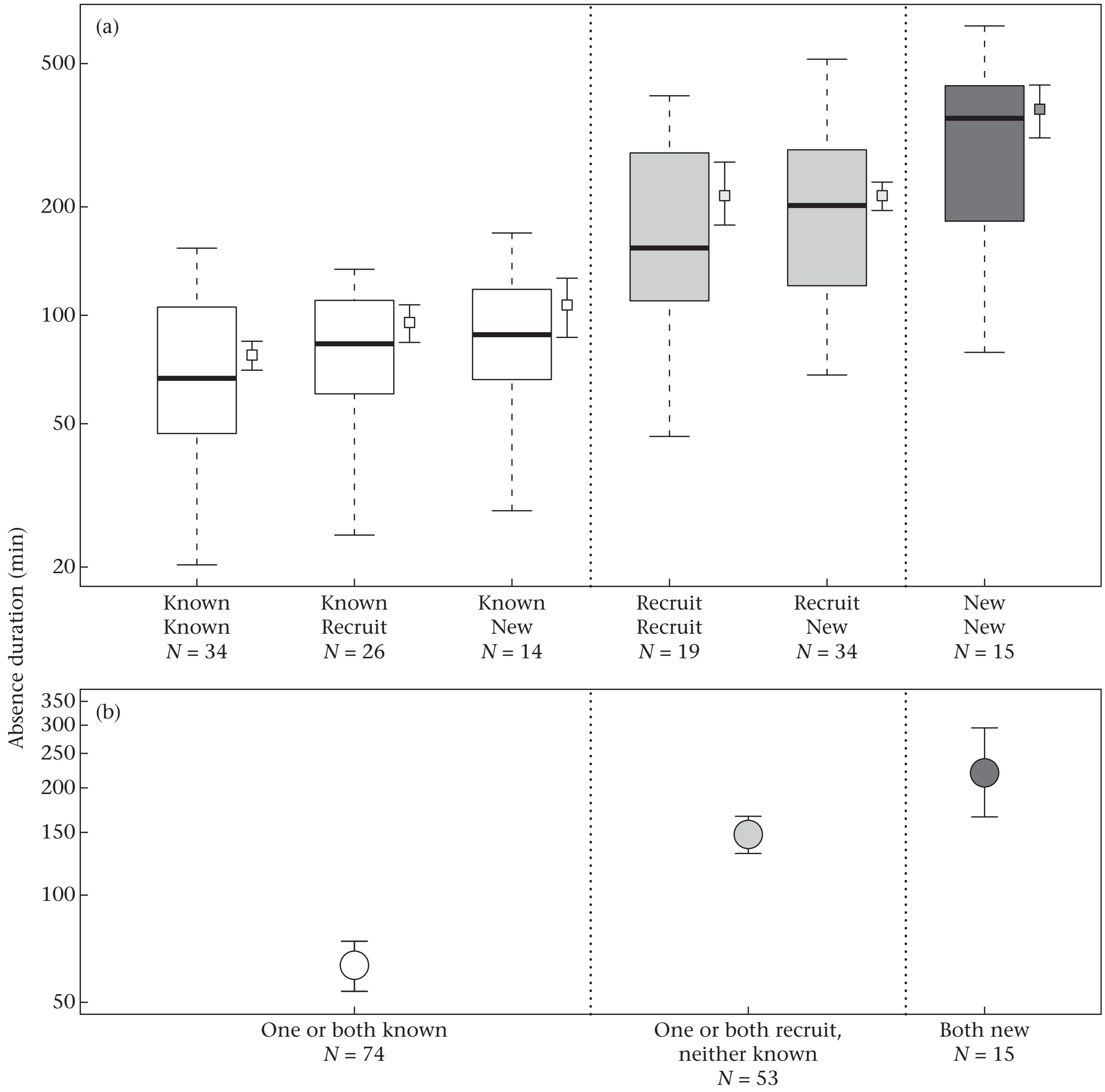

Figure 2. Influence of pair capture status on absence durations (in min, nights removed). (a) Box plots (thick line: median; hinges: 25th and 75th quartiles; whiskers: range of the data points excluding outliers); the label on the x-axis gives the combination of capture status of the two individuals in a pair; squares with error bars next to boxes give mean and SE; note the log-scale on the y-axis. (b) Model estimates (model 1) and their 95% confidence region; note the log-scale on the y-axis.

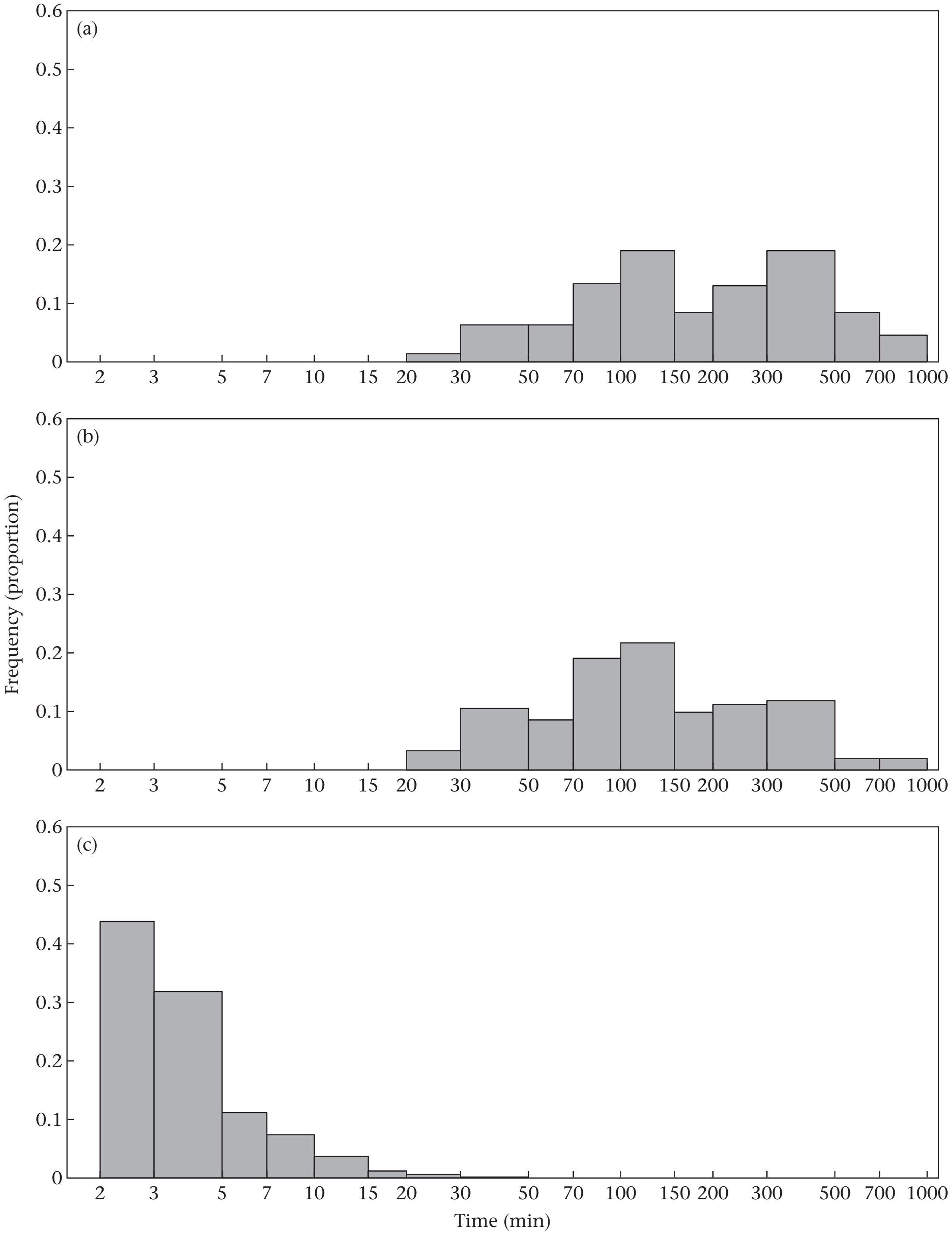

Figure 3. Distribution of (a) individual return latencies after capture (adjusted to exclude nights; $N = 284$), (b) parental absence durations at nest induced by capture (adjusted to exclude nights; $N = 152$) and (c) natural absences between visits of parents ($N = 81\,435$). Note the log-scale on the x-axes.

Fair et al., 2010) on the nestbox visit behaviour of blue tits feeding nestlings. We found that after CHMS parents returned to the nest only after a surprisingly long time, on average 4.2 h. These absence durations are much longer than those observed after a simple disturbance at the nest (checking the nest during the nestling period). This result highlights that CHMS disturbances may alter immediate behaviour of individuals for a substantially longer period than is generally assumed (Calvo & Furness, 1992; Duarte, 2013, chapter 2; Murray & Fuller, 2000).

General Explanations for Long Return Latencies

Although known birds were subjected to a noninvasive protocol, they showed long return latencies of, on average, 2 h. Most reports on behaviour after capture are incidental (Murray & Fuller, 2000). Systematic investigations of behaviours shortly after capture all point to effects lasting several hours, but have employed a range of procedures, all using fairly traumatic methods of trapping (Burger et al., 1995; Frederick, 1986; Nisbet, 1981, 2000; Olsen & Schmidt,

Table 4
Effects of adjusted absence duration (in min, night excluded) on brood traits and breeding success of blue tits

Response variable	Estimate (95% CI)	*P*
Duration of nestling period (days between capture and fledging)[1]	-0.1×10^{-3} (-1.0×10^{-3} to 0.8×10^{-3})	0.79
Brood tarsus (averaged among nestlings, (mm))[1]	-2.0×10^{-4} (-5.2×10^{-4} to 0.9×10^{-4})	0.20
Brood weight (averaged among nestlings, (g))[1]	-1.7×10^{-4} (-4.8×10^{-4} to -7.6×10^{-4})	0.58
Brood condition (averaged among nestlings, weight (g)/tarsus (mm))[1]	-0.4×10^{-5} (-3.2×10^{-5} to 3.1×10^{-5})	0.79
Proportion of nestlings fledged[2]	0.6×10^{-2} (-0.9×10^{-2} to 2.0×10^{-2})	0.41
Probability of brood failure[2]	3.9×10^{-3} (-0.8×10^{-3} to 7.0×10^{-3})	0.99

In all models, identity of the focal individual and brood identity were included as random variables.

[1] Linear mixed-effects model (LME), with year as fixed effect (details not shown).

[2] General linear mixed model (GLMM) with binomial error structure, and with year as fixed effect (details not shown).

2001). In songbirds, reduced feeder attendance and incubation effort after capture in mist nets have been reported in two small-scale studies (Duarte, 2013, chapter 3: $N = 32$, seven species; Duarte, 2013, chapter 5: $N = 12$, six species). In line with our results, the second study found that latency to resume incubation was substantial and varied widely between individuals (mean 104 min, range 14–319 min) and that levels of incubation went back to previous levels shortly after (Duarte, 2013, chapter 5). Thus, both studies provide evidence that the common notion that return latencies after CHMS disturbance during the breeding season are short, because birds generally quickly resume ‘parental duties’, is not always correct. At the same time, both studies suggest that, once returned, birds do resume parental duties in a normal fashion. However, there are important differences even between closely related species (Nisbet, 1981) and between different populations of the same species (Burger et al. 1995). The latter may partially be a result of local selection across the high interindividual differences as found in this study, whereby individuals less resilient to human disturbance are located in populations that are little exposed to it (Murray & Fuller, 2000). The immediate changes in behaviour after noninvasive CHMS in our study could be due to disturbance by humans as such, general and stress recovery or reaction to perceived predation.

Behavioural consequences of human presence (e.g. visits by scientists or tourists) have been considered in a number of studies (Beale & Monaghan, 2004; Culik et al., 1990; Fair et al. 2010; Frid & Dill, 2002; Götmark, 1992; Keller, 1995) and reports of negative impacts are typically from birds that, unlike blue tits, nest in open habitat and/or in colonies, where exposure to humans and their potential threat is highest and researchers cannot easily prevent general disturbance while they are working with a particular bird at the study site (Götmark, Neergaard, & Åhlund, 1989; Sandvik & Barrett, 2001; Verboven, Ens, & Dechesne, 2001). It is unlikely that researcher presence was decisive for the prolonged return latencies in this study, because birds remained absent when humans had long left the territory. Absence durations for nests, even where both parents were known birds, were about 20 times longer than the natural intervals, and average return latencies were at least 2 h for all treatment groups, while return latencies after nest checks were on average 10 min.

Birds may perceive capture as a predation event (Beale & Monaghan, 2004; Duarte, 2013, chapter 3; Frid & Dill, 2002; Gosler, 2001; Laiolo et al., 2009; MacLeod & Gosler, 2006; Wilson & McMahon, 2006) and react by avoiding the location of capture (the nest), returning only after they have assessed the predation risk to be reduced again to before-capture levels. This could explain why normal visiting patterns re-emerge, once parents have returned.

One of the most important consequences of CHMS is triggering a general physiological stress response. Based on studies utilizing the capture–handling–restraint protocol, CHMS causes a substantial physiological stress response that can last several hours (Deviche, Gao, Davies, Sharp, & Dawson, 2012; Le Maho et al., 1992; Remage-Healey & Romero, 2001). Recovery from stress may be especially important if CHMS is the perceived predation event mentioned above. Similarly, pain, irritation or specific physiological changes induced by the procedures applied to recruits and new birds may involve or increase a generalized stress response, while previous capture experience (known birds) or handling by humans (recruits) may alleviate the stress in the current CHMS event. Behavioural effects of stress (Sapolsky, Romero, & Munck, 2000) may have caused a disruption of nest visit behaviour in our study. However, an experimental study in blue tits (Schlicht, Geurden, & Kempenaers, n.d.) found no behavioural indicators of stress (tumultuous flights, hectic, fluffing, squinting, lethargy; Gentle & Hunter, 1991; Machin, 2005; Woolley & Gentle, 1987), either in birds subjected to capture, handling, measuring and ringing or in birds that were additionally sampled for blood and PIT-tagged.

For all birds CHMS represents a harsh interruption of considerable duration (in our study 30 min on average) of their normal behavioural schedule. After such an event, birds may thus alter their behaviour to replenish energy (foraging, resting) before returning to the nestbox. In line with this, birds resumed normal nest attendance once they had returned. The results from the experimental study (Schlicht et al., n.d.) also showed a fast initiation of feeding (on average 4 min after release).

Differences Between Treatment Groups

One interesting result of our study is the marked difference in return latencies (nights removed) between known birds (1.9 h), recruits (5.0 h) and new birds (6.3 h), and the associated different absence durations. Although field protocols of many studies involve capture of previously marked and new birds, differences due to variation in treatment (only new birds are marked and sampled) are usually not considered (e.g. MacLeod & Gosler, 2006).

In our study, the procedures of feather clipping (in 2010), blood sampling, implantation of PIT tags and ringing with colour rings were applied only to recruits or new birds, and the procedure of ringing with a metal ring was applied only to new birds. Longer return latencies in new birds and recruits compared to known birds may be the result of the physiological changes, pain or irritation associated with the additional procedures. It is also possible that known birds represent a subsample of individuals particularly resilient to CHMS. However, new birds resumed normal visit patterns once they had returned, and breeding success was not impaired. It is therefore unlikely that the effects of CHMS carry over to consecutive breeding seasons with more sensitive individuals not breeding again in the study area.

In this study, the physiological impact of blood sampling (Brown & Brown, 2009; Fair et al., 2010; Voss, Shutler, & Werner, 2010) is probably small, given that we usually sampled less than 10% of the volume that is considered a safe margin (Fair et al., 2010). Symptoms indicative of problems associated with the drawing of blood (e.g. breathlessness, reduced level of consciousness) were never observed. Still, mild physiological consequences may have induced fatigue and reduced physical endurance, prolonging the time until the bird resumes normal behaviour. Behavioural consequences of blood sampling have rarely been inspected, but on a day-to-day basis no effects have been found (Angelier et al., 2010; Ardern et al., 1994; Frederick, 1986).

Both blood sampling and implantation of PIT tags involve local skin lesions. These should be too small to affect the physiological function of the integument. Little is known about the immediate behavioural consequences of tag implantation in wild birds. No effects have been found in studies comparing behaviour across days (Ballard, Ainley, Ribic, & Barton, 2001; Dugger, Ballard, Ainley, & Barton, 2006; Keiser, Ziegenfus, & Cristol, 2005; Ludynia et al., 2012).

Blood sampling and tag insertion are associated with pain. Extrapolating from the pain associated with venepuncture in mammals (Carstens & Moberg, 2000; Gentle, 2011; Machin, 2005), it would represent a very brief, acute pain event, which is experienced as slight to mild in most cases, occasionally as moderate (Agarwal, Sinha, Tandon, Dhiraaj, & Singh, 2005; Lavery & Ingram, 2005; Patterson, Hussa, Fedele, Vegh, & Hackman, 2000; Selby & Bowles, 1995). No such information is available for tag implantation, but the anatomy (Stettenheim, 2000; Weir & Lunam, 2011), innervation and central nervous representation of the skin of the back (Kuenzel, 2007; Wild, Reinke, & Farabaugh, 1997) suggest relatively low sensitivity. Based on this, we expect the pain associated with tag implantation in most cases to be moderate and always brief. In our study, we never observed pain-related behaviour (squinting, fluffing, lethargy; Gentle, 1992, 2011; Machin, 2005) during handling of birds and all birds flew off normally upon release. In the experimental study on blue tits (Schlicht et al., n.d.), changes in respiration rate, expected under pain (Wilson & McMahon, 2006; Woolley & Gentle, 1987), did not occur during any procedure, including blood sampling and PIT tagging. No pain-related behaviours were observed during or following treatment.

Results from a study on roseate terns, *Sterna dougallii*, and common terns, *Sterna hirundo*, showed a drastic increase in bathing and preening over several hours after capture and ringing for one species (roseate tern). The additional application of patagial tags doubled the latency to return to the nest area by common terns (Nisbet, 1981). It is possible that in the present study bleeding, and the application of PIT tags and rings, similarly induced skin sanitation behaviour to a degree that it substantially delayed foraging and returning to the nest. In addition, preening and related behaviours may last longer in an attempt to remove the newly attached rings and transponder. Blue tits can reach their leg rings, but not the site of tag insertion with their beaks. In both cases, it is possible that their behavioural routine is interrupted repeatedly due to annoyance associated with the altered sensation of the epithelium. In the experimental study in blue tits (Schlicht et al., n.d.), ring pecking was the primary behavioural alteration after CHMS, and the results suggested that immediate behavioural effects of PIT tagging and blood sampling are not more important than the attachment of rings. Attempts to remove leg rings have been reported anecdotally for a number of species (Burton, 2001; Calvo & Furness, 1992; Hill & Talent, 1990; Kosinski, 2004; Lovell, 1948; Ludwig, 1967; Nisbet, 1981; Poulding, 1954; Reese, 1980; Stedman, 1990; Young, 1941).

Biological Implications

Interestingly, we did not find any long-term effects of CHMS in terms of breeding success and brood fitness, despite surprisingly long parental absences. This reveals that 9- or 10-day-old young seem resilient against fluctuations in food supply. This might be an adaptation to occasional low feeding rates, for example due to a longer spell of bad weather (Kunz & Ekman, 2000). When broods fail after capture, this is usually interpreted as nest desertion, that is, parents failing to return to the nest after capture. An alternative explanation is that parents do return, but that their absence has been too long for the young to survive. In this study, all nestlings of 12 broods (5%) were found dead at the nest check closest following capture, suggesting that brood failures directly after capture are rare if parents do return. Note that this estimate is the upper limit, because we usually performed the next nest check 5 days after capture (2 days for two nests), so we are unable to determine when exactly brood failure occurred.

Return latencies were not linked to individual traits, and we found no evidence of within-individual repeatability. However, effects of CHMS were not completely unrelated to the biological background. We found that absences were longer when parents raised larger broods or broods in better condition. This suggests that delay in return does not primarily reflect parental ability (because then the opposite effect would have been predicted, assuming that brood size and condition are positively related to parental condition). Instead, parents may delay their return when they can ‘afford’ it, i.e. when their or their offspring's condition allows them to ‘catch up’ after longer absences without detrimental long-term fitness effects.

Methodological Implications

The unexpectedly long return latencies observed in this study as a result of CHMS are of relevance for the field in two ways. First, animal welfare considerations should prompt researchers to renew their effort to improve current CHMS procedures (Cazaux, 2007). A variety of methods for capture, blood sampling, marking, tagging and tracking are available with recent novelties and ongoing technological progress (Bonter & Bridge, 2011; Fair et al., 2010; Murray & Fuller, 2000; Owen, 2011; Watson, 2012; Wellbrock, Bauch, Rozman, & Witte, 2012).

Second, our findings of immediate impacts of CHMS provide valuable information for researchers planning experiments, compiling data sets and interpreting results. The general occurrence of unexpectedly long return latencies shows that even when manipulations are minimized (e.g. only ringing) capture can have strong effects on immediate behaviour. On the other hand, even the most sensitive birds apparently resume parental care normally after returning to the nest. The design and methods of our long-term study are widely used in studies of avian behaviour (e.g. García-Navas & Sanz, 2011; Limbourg, Mateman, & Lessells, 2013; Mahr, Griggio, Granatiero, & Hoi, 2012). Here, alternatives to capturing adults on the nests are usually not available, but it is important to be aware of its short- and long-term impacts. For example, in line with our previous experience that capture late in the day increased the probability of brood failure, we found an increase in absence duration with capture time. It is possible that these instances are the result of parental absences too long for the young to deal with, because shortly afterwards they again have to survive the overnight food deprivation. In general, feeding rates are clearly affected much more strongly by disturbances than is commonly acknowledged (e.g. García-Navas & Sanz, 2011; Limbourg et al., 2013; Mahr et al., 2012).

Our results are also relevant for studies using automated tracking devices. The findings suggest that collection of meaningful data cannot start as early as is often assumed. However, automated data collection also minimizes the number of captures needed to collect specific types of data. While longer return latencies in recruits and new birds may in part be due to tag implantation, the long return latencies even in previously caught birds indicate that every capture has pronounced short-term effects on the individual. No damaging consequences of tag implantation on condition, survival or fitness have been found in numerous studies (Fair et al., 2010; Nicolaus et al., 2008; Schroeder & Cleasby, 2011), and we have shown here that birds adopted normal feeding behaviour once they had returned to the nest, that nestlings could deal well even with prolonged periods of parental absence, and that no fitness reductions in terms of nest failure or partial brood mortality were associated with absence durations. We therefore advocate the use of automated logging devices, whenever this reduces the number of times an individual needs to be caught. It is not feasible to study animal behaviour without impact, but these methods come closest to virtually disturbance-free data collection.

Conclusion

This study investigated behaviour of wild blue tits immediately after capture. Our results indicate substantial effects on behaviour in that birds failed to return to provision the nestlings over a period of several hours. Methods typically used in ornithological studies may thus have considerable consequences. These consequences are difficult to predict, because even closely related species may differ substantially in their response to capture and handling. In our study, once the parents returned, they assumed normal behaviour without further delay, and no long-term effects of parental absence due to CHMS were found. While researchers should be aware of the strong immediate effects they can impose with CHMS on birds, and of the potential biases induced by differential procedures during CHMS, the assertion that birds ultimately return to normal behaviour appears to hold.

Acknowledgments

We thank Agnes Türk for the initial suggestion to conduct this study. We are grateful to Alexander Girg for genotyping, to Peter Loës and Peter Skripsky for development and maintenance of the nestbox loggers, to Lotte Schlicht, Agnes Türk and Andrea Wittenzellner for fieldwork, to Jonas Geurden for discussion and to Angela Turner for improving the writing. Four anonymous referees provided comments that greatly improved the manuscript. This work is funded by the Max Planck Society.

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APPENDIX 1

Brood size refers to the number of young at the time of capture and laying date to the date on which the first egg of the clutch was laid. As is often the case (Decker, Conway, & Fontaine, 2012), these variables were strongly correlated, such that broods with an early lay date were larger (change in number of young per day delay: −0.19 (−0.24 to −0.14), $P < 0.001$; linear mixed-effect model with identity of parent and nestbox as random factors and year as covariate). Initially we inspected effects of both variables separately and in conjunction and found no additional explanatory effect by one variable over the other or in combination. We also replaced brood size with clutch size and with number of young fledged in all analyses and results did not change qualitatively. The same was true for using hatching or fledging date instead of lay date. We therefore only included brood size in all consecutive analyses, because it seems biologically most relevant for the situation at capture.

APPENDIX 2

Condition was calculated as the ratio of weight over tarsus (Barthelmess, 2006; Labocha, Schutz, & Hayes, 2014; Pitt, Larivière, & Messier, 2006). There was no evidence that weight–tarsus allometry influenced condition estimates: fitting a curve to the weight over tarsus via a cubic smoothing spline (R-package ‘fields’; Furrer, Nychka, & Sain, 2013) resulted in a straight line; no transformation of variables was necessary to meet assumptions of homogeneity of variance and normality in the Model 1 (ordinary least squares) regression of weight over tarsus (Jakob, Marshall, & Uetz, 1996). The two body size measurements taken, primary length and tarsus, led to similar results, indicating that variation in tarsus length reflects structural size (Green, 2001). Using residuals of either Model 1 (Schulte-Hostedde, Zinner, Millar, & Hickling, 2005) or Model 2 (here: ranged and standard major axis; Green, 2001) regression instead of ratios did not affect results qualitatively (Pearson's r between ratio and both residual measurements >0.92).

Appendix 3

Table A1
Annual sample sizes for individual blue tits, divided by sex, age (yearling or older), breeding experience on the study site and capture status

	2010	2011	2012	Total
Number of birds	80	77	127	284 (255)
Males	42	38	62	142 (128)
Yearlings	48	23	84	155 (155)
Previous breeders	19	43	26	88 (77)
Capture status: ‘known’	27	46	33	106 (92 individuals)
Capture status: ‘recruit’	22	17	59	98
Capture status: ‘new’	31	14	35	80
Ratio capture status (‘known’):(‘uncaught’)	0.5	1.5	0.4	0.6

Some birds were caught in more than 1 year (2010 and 2011: $N = 8$; 2010 and 2012: $N = 4$; 2011 and 2012 $N = 13$; 2010, 2011 and 2012: $N = 2$; number of unique individuals given in parentheses). ‘Capture status’ refers to the previous capture and handling experience of the bird (‘known’ = bird known from previous captures, ‘recruit’ = local recruit, ‘new’ = new bird). The status ‘uncaught’ refers to local recruits and new birds combined. The proportion of uncaught birds varied significantly between all three study years (all $\chi^2 > 153$, all $P < 0.001$).

Table A2
Effects of capture status on retention time, return latencies and absence durations

	Variable		Estimate (95% CI)	*P* (MCMC)
Retention time explained by capture status[1]				
	(Intercept)		35.26 (32.24 to 38.88)	(<0.001)
	Capture status[1] (‘known’) versus (‘uncaught’)		−4.00 (−6.54 to −1.11)	0.006
	Year	2011 versus 2010	6.00 (3.26 to 10.50)	<0.001
		2012 versus 2010	−10.96 (−14.41 to −7.60)	<0.001
		2012 versus 2011[4]	*−18.15 (−21.13 to −15.20)*	*<0.001*
Return latency explained by ratio capture status[2]				
	(Intercept)		5.53 (5.34 to 5.71)	(<0.001)
	Ratio capture status (‘known’):(‘uncaught’)		−0.49 (−0.70 to −0.30)	<0.001
Absence duration explained by ratio capture status[3]				
	(Intercept)		5.12 (5.00 to 5.33)	(<0.001)
	Ratio capture status (‘known’):(‘uncaught’)		−0.45 (−0.60 to −0.27)	<0.001

The table shows the influence of capture status[1] on retention time (min; note that the year effects mainly come about by annual variation in protocol, while capture status is less influential) and of annual variation in proportion of known birds (ratio capture status, see Table A1) on adjusted return latencies[2] and adjusted absence durations[3] (both min, log-transformed). All models are LMEs where the identity of the focal individual and brood identity were included as random variables.

[1] Capture status: ‘known’ = bird caught previously; ‘recruit’ = bird hatched on study site and not caught previously; ‘new’ = unknown bird; ‘uncaught’ = recruits and new birds.

[2] Return latencies after capture, adjusted to exclude duration of night for birds returning on the next day (see Methods).

[3] Duration of time that the nestbox was not attended by any parent; adjusted to exclude duration of night for intervals covering the next day (see Methods).

[4] The comparison between years 2011 and 2012 is shown in italics, because it was extracted from a model in which the variable ‘year’ was recoded to include this comparison (i.e. different intercept).

Table A3
Results of full model (LME) for adjusted return latencies (Model 3)

Variable		Estimate (95% CI)	Back-transformed estimate[1] (95% CI)	*P* (MCMC)
	(Intercept)	4.46 (4.03 to 4.89)	86.08 (56.52 to 133.13)	<0.001
	Year 2011 versus 2010	+0.17 (−0.18 to 0.54)	×1.19 (0.83 to 1.71)	0.36
	Year 2012 versus 2010	+0.41 (0.15 to 0.67)	×1.51 (1.17 to 1.96)	<0.001
A[2]	Sex (female versus male)	+0.05 (−0.14 to 0.24)	×1.05 (0.87 to 1.27)	0.63
	Age (older versus yearling)	−0.14 (−0.40 to 0.13)	×0.87 (0.67 to 1.14)	0.31
	Tarsus (mm)	+0.04 (−0.14 to 0.20)	×1.04 (0.87 to 1.23)	0.65
	Weight (g)	−0.06 (−0.22 to 0.13)	×0.94 (0.81 to 1.13)	0.50
	Recruit (yes versus no)	−0.05 (−0.33 to 0.26)	×0.95 (0.72 to 1.30)	0.73
	Previous breeding experience (yes versus no)	+0.00 (−0.39 to 0.40)	×1.00 (0.68 to 1.50)	0.97
B[2]	Brood size	+0.00 (−0.05 to 0.05)	×1.00 (0.95 to 1.05)	0.89
	Brood contains extrapair young (yes versus no)	+0.08 (−0.08 to 0.26)	×1.09 (0.93 to 1.29)	0.31
	Mean tarsus length of chick in brood (mm)	−0.12 (−0.33 to 0.10)	×0.89 (0.72 to 1.10)	0.29
	Mean condition of chick in brood (weight in g/tarsus in mm)	+1.99 (−0.42 to 4.42)	×7.35 (0.66 to 83.02)	0.11
C[2]	Capture date (days)	+0.04 (0.00 to 0.08)	×1.04 (1.00 to 1.08)	0.03
	Capture time (h)	+0.05 (−0.01 to 0.11)	×1.05 (0.99 to 1.11)	0.09
	Capture order (second versus first caught bird at nest)	−0.08 (−0.28 to 0.08)	×0.92 (0.76 to 1.08)	0.37
	Retention time (min)	+0.01 (0.00 to 0.02)	×1.01 (1.00 to 1.02)	0.02
	Capture status[3] (recruit versus new)	+0.70 (0.27 to 1.15)	×2.02 (1.32 to 3.15)	<0.001
	Capture status (known versus new)	+1.02 (0.65 to 1.43)	×2.78 (1.91 to 4.18)	<0.001
	Capture status (known versus recruit)[4]	*+0.31 (−0.03 to 0.67)*	*×1.37 (0.97 to 1.95)*	*0.08*

Response variable is the latency of return to the nest of individual parents in min (night excluded; log-transformed). Identity of focal individuals and brood identity were included as random variables.

[1] After back-transformation from log-scale, the effect is indicated by a factor (×1 indicates no difference).

[2] Explanatory variables linked to the focal individual (A), to the brood (B) and to handling (C, see Methods).

[3] ‘Capture status’ refers to the previous capture and handling experience of the bird (‘known’ = bird known from previous captures, ‘recruit’ = local recruit, ‘new’ = new bird).

[4] The comparison between capture status ‘new’ and ‘recruit’ is shown in italics, because it was extracted from a model in which the variable ‘capture status’ was recoded to include this comparison (i.e. different intercept).

Table A4
Results of reduced combined model (LME) for adjusted return latencies (Model 2), identical to reduced full model (Model 4)

Variable		Estimate (95% CI)	Back-transformed estimate[1] (95% CI)	*P* (MCMC)
	(Intercept)	4.39 (4.21 to 4.55)	80.37 (67.07 to 95.10)	(<0.001)
	Year 2011 versus 2010	+0.04 (−0.18 to 0.23)	×1.04 (0.84 to 1.26)	0.66
	Year 2012 versus 2010	+0.37 (0.17 to 0.54)	×1.44 (1.19 to 1.72)	<0.001
C[2]	Capture status[3] (recruit versus known)	+0.83 (0.64 to 1.01)	×2.30 (1.89 to 2.75)	<0.001
	Capture status (new versus known)	+1.19 (0.99 to 1.38)	×3.28 (2.69 to 3.97)	<0.001
	Capture status (new versus recruit)[4]	*+0.35 (0.15 to 0.55)*	*×1.43 (1.16 to 1.74)*	*<0.001*

Response variable is the latency of return to the nest of individual parents in min (night excluded; log-transformed). Identity of focal individuals and brood identity were included as random variables.

[1] After back-transformation from log-scale, the effect is indicated by a factor (×1 indicates no difference).

[2] Explanatory variables linked to handling (see Methods).

[3] ‘Capture status’ refers to the previous capture and handling experience of the bird (‘known’ = bird known from previous captures, ‘recruit’ = local recruit, ‘new’ = new bird).

[4] The comparison between capture status 2 (new bird) and 1 (recruit) is shown in italics, because it was extracted from a model in which the variable ‘capture status’ was recoded to include this comparison (i.e. different intercept).

Table A5
Results of full model (LME) for adjusted absence duration (Model 3)

Variable		Estimate (95% CI)	Back-transformed estimate[1] (95% CI)	*P* (MCMC)
	(Intercept)	4.24 (4.05 to 4.42)	69.57 (57.37 to 83.22)	(<0.001)
	Year 2011 versus 2010	−0.05 (−0.35 to 0.24)	×0.95 (0.70 to 1.27)	0.75
	Year 2012 versus 2010	+0.39 (0.24 to 0.52)	×1.47 (1.27 to 1.68)	<0.001
A[2]	Age (older versus yearling)	+0.01 (−0.06 to 0.09)	×1.01 (0.94 to 1.09)	0.80
	Tarsus (mm)	+0.02 (−0.03 to 0.09)	×1.02 (0.97 to 1.09)	0.43
	Weight (g)	−0.03 (−0.09 to 0.05)	×0.97 (0.91 to 1.05)	0.40
B[2]	Brood size	+0.04 (0.01 to 0.08)	×1.04 (1.01 to 1.08)	0.02
	Brood contains extrapair young (yes versus no)	−0.09 (−0.23 to 0.03)	×0.92 (0.80 to 1.03)	0.17
	Mean tarsus length of chick in brood (mm)	−0.03 (−0.20 to 0.11)	×0.97 (0.82 to 1.12)	0.69
	Mean condition of chick in brood (weight in g/tarsus in mm)	+2.35 (0.81 to 3.98)	×10.49 (2.24 to 53.75)	0.004
C[2]	Capture date (days)	+0.02 (−0.01 to 0.05)	×1.02 (0.99 to 1.05)	0.22
	Capture time (h)	+0.07 (0.04 to 0.10)	×1.07 (1.04 to 1.10)	<0.001
	Retention time (min)	+0.00 (0.00 to 0.01)	×1.00 (1.00 to 1.01)	0.14
	Pair capture status[3] (1 versus 0)	+0.74 (0.60 to 0.85)	×2.1 (1.83 to 2.33)	<0.001
	Pair capture status (2 versus 0)	+1.61 (1.42 to 1.80)	×5.00 (4.15 to 6.07)	<0.001
	Pair capture status (2 versus 1)[4]	*+0.85 (0.64 to 1.05)*	*×2.35 (1.9 to 2.85)*	*<0.001*

Response variable is the total absence duration of both parents at the nest in min (night excluded; log-transformed). Identity of focal individuals and brood identity were included as random variables.

[1] After back-transformation from log-scale, the effect is indicated by a factor (×1 indicates no difference).

[2] Explanatory variables linked to the focal individual (A), to the brood (B) and to handling (C, see Methods).

[3] 'Pair capture status' refers to the joint capture and handling experience of the pair (status 0: at least one of the birds was known from previous captures; status 1: none of the birds were known, but at least one was a local recruit; status 2: both birds were new).

[4] The comparison between pair capture status 2 (both birds new) and 1 (at least one recruit, none known) is shown in italics, because it was extracted from a model in which the variable 'pair capture status' was recoded to include this comparison (i.e. different intercept).

Table A6
Results of reduced combined model (LME) for adjusted absence durations (Model 2), identical to reduced full model (Model 4)

Variable		Estimate (95% CI)	Back-transformed estimate[1] (95% CI)	*P* (MCMC)
	(Intercept)	4.27 (4.11 to 4.42)	71.82 (61.11 to 82.94)	(<0.001)
	Year 2011 versus 2010	−0.18 (−0.35 to −0.03)	×0.84 (0.70 to 0.97)	0.04
	Year 2012 versus 2010	+0.33 (0.23 to 0.47)	×1.40 (1.26 to 1.59)	<0.001
B[2]	Brood size	+0.04 (0.01 to 0.07)	×1.04 (1.01 to 1.08)	0.01
	Mean condition of chick in brood (weight in g/tarsus in mm)	+1.74 (0.33 to 3.27)	×5.69 (1.39 to 26.24)	0.02
C[2]	Capture time (h)	+0.06 (0.03 to 0.08)	×1.06 (1.03 to 1.09)	<0.001
	Pair capture status[3] (1 versus 0)	+0.74 (0.61 to 0.85)	×2.09 (1.85 to 2.33)	<0.001
	Pair capture status (2 versus 0)	+1.66 (1.48 to 1.84)	×5.27 (4.40 to 6.28)	<0.001
	Pair capture status (2 versus 1)[4]	*+0.93 (0.74 to 1.11)*	*×2.52 (2.11 to 3.02)*	*<0.001*

Response variable is the total absence duration of both parents at the nest in min (night excluded; log-transformed). Identity of focal individuals and brood identity were included as random variables.

[1] After back-transformation from log-scale, the effect is indicated by a factor (×1 indicates no difference).

[2] Explanatory variables linked to the brood (B) and to handling (C, see Methods).

[3] 'Pair capture status' refers to the joint capture and handling experience of the pair (status 0: at least one of the birds was known from previous captures; status 1: none of the birds were known, but at least one was a recruit; status 2: both birds were new).

[4] The comparison between pair capture status 2 (both birds new) and 1 (at least one recruit, none known) is shown in italics, because it was extracted from a model in which the variable 'pair capture status' was recoded to include this comparison (i.e. different intercept).

Table A7
Effect of capture on duration of natural occurring gaps between nest visits (min)

	Variable	Estimate (95% CI)	Back-transformed estimate[1] (95% CI)	*P*
Day of capture	(Intercept)	1.46 (1.15 to 1.76)	4.29 (3.17 to 5.80)	(<0.001)
	After versus before capture	+0.10 (0.06 to 0.13)	×1.10 (1.06 to 1.14)	<0.001
Day of capture (last visits excluded)	(Intercept)	1.45 (1.34 to 1.55)	4.25 (3.83 to 4.72)	(<0.001)
	After versus before capture	+0.01 (−0.04 to 0.0)	×1.01 (0.96 to 1.05)	0.69
Day preceding capture	(Intercept)	1.48 (1.31 to 1.65)	4.39 (3.71 to 5.19)	(<0.001)
	'After' versus 'before' interval corresponding to capture	+0.11 (0.07 to 0.15)	×1.12 (1.07 to 1.16)	<0.001
'After' time interval on both days	(Intercept)	1.61 (1.34 to 1.89)	5.00 (3.80 to 6.59)	(<0.001)
	Capture day versus previous day	−0.62 (−2.66 to −0.11)	×0.94 (0.90 to 0.07)	<0.001

Comparison of gaps before and after capture on the capture day for all visits and excluding the last 10 gaps of the capture day, in corresponding intervals on the day preceding capture and on the capture day after capture and in the corresponding time interval of the preceding day. GLMMs with Poisson error structure. Identity of focal brood and year were included as random variables.

[1] After back-transformation from log-scale, the effect is indicated by a factor (×1 indicates no difference).

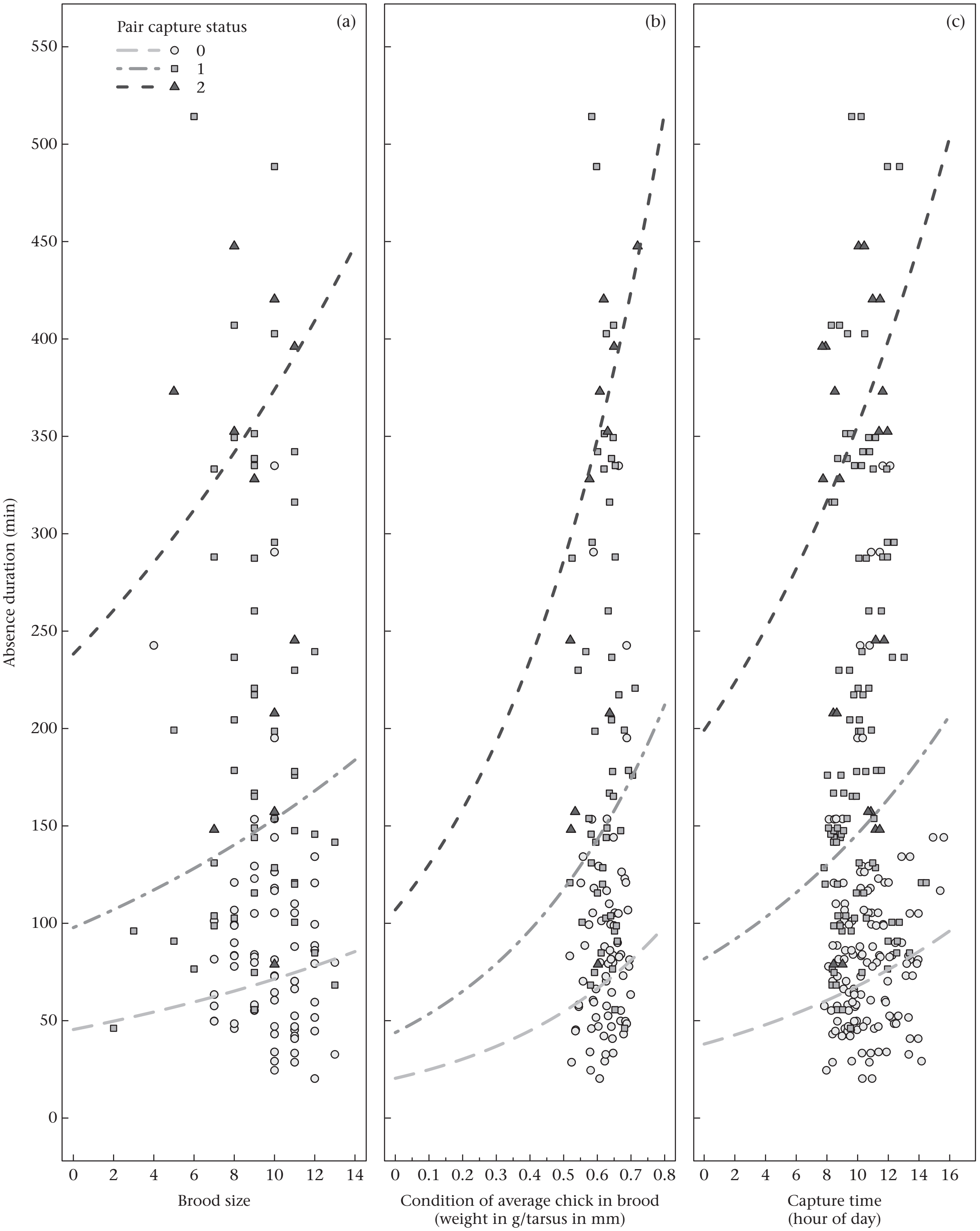

Figure A1. Effect of (a) brood size, (b) brood condition and (c) capture time on the total absence duration of both parents at the nest (night excluded). Lines fitted from model 1 (Table 3, main text) and separated by pair capture status (0: at least one parent known, $N = 82$; 1: at least one parent is a local recruit, but neither is known, $N = 57$; 2: both parents new, $N = 15$). Note that points in (a) and (b) represent nests (brood size and condition are the same for both parents) whereas points in (c) represent parents (capture times differ between parents). Inclusion of nest and individual ID as random factors in the model controls for pseudoreplication in the test of (c).

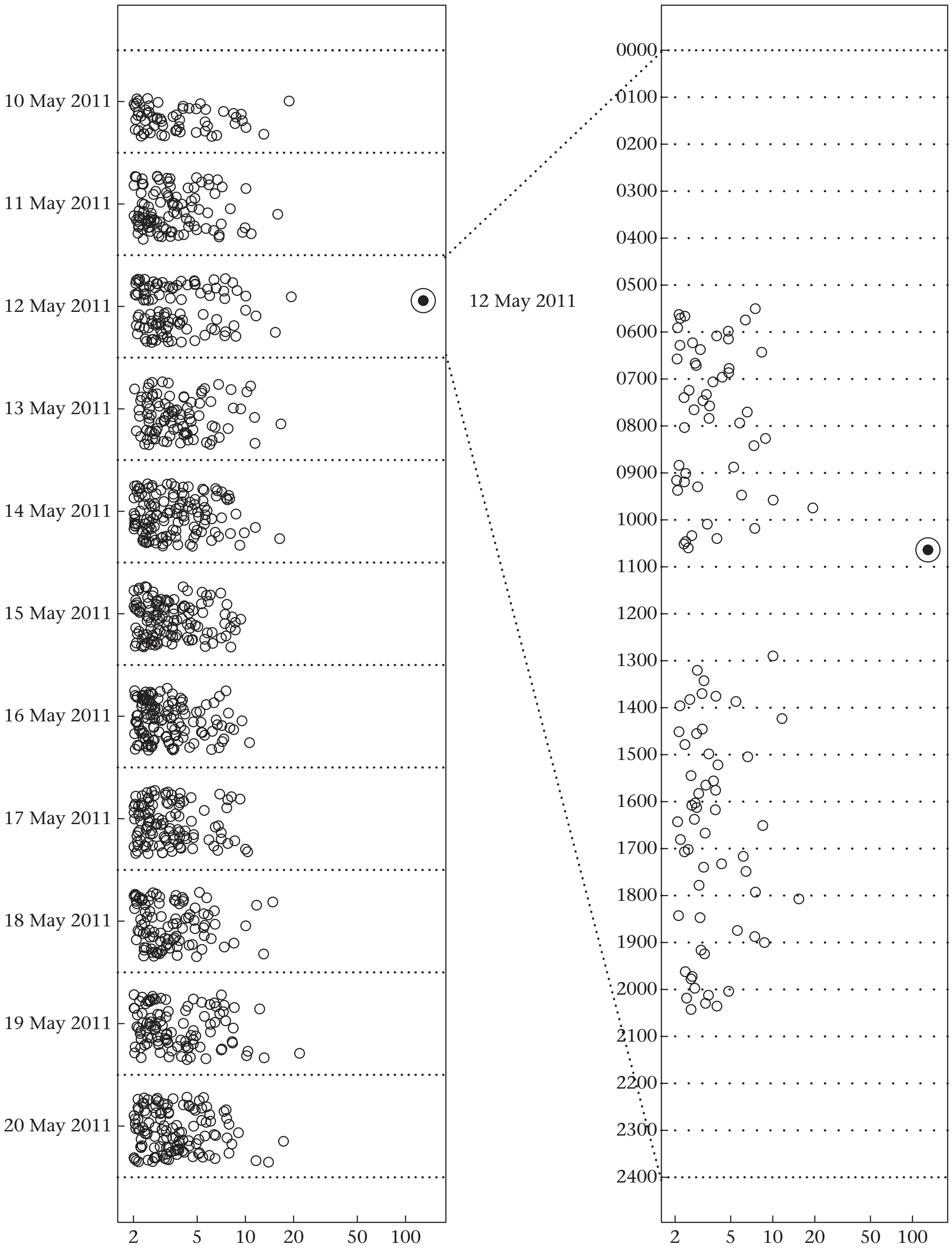

Figure A2. Example of a typical pattern of parental absence durations. (a) Absence durations over 11 days for one nest (box 166) in 2011. Natural absence durations (open points) are much shorter than the capture-induced absence duration (dot, highlighted by a circle). The day of capture (12 May) is shown blown up in (b). Note the log-scale on the x-axes.