1 Commentary

2 Lifelong effects of trapping experience lead to age-biased sampling: lessons from a wild
3 bird population

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Long-term monitoring of individually marked animals is usually required for reliable estimation of numerous life history parameters. However, capture, marking and manipulation can dramatically alter the animals' behaviour after capture, and thus affect subsequent recapture success. Here, we used a pied flycatcher, *Ficedula hypoleuca*, population as an example to illustrate the sampling bias resulting from the repeated capture of free-ranging individuals. By using repeated measures of the same individuals obtained during our long-term survey, we specifically evaluated the interannual response of breeding adults to capture-related stress, measured as latency to enter nestboxes equipped with a swing-trap. Moreover, we examined changes in the mean and variance of bird age with varying trapping effort using subsamples of the data set. Birds without any previous trapping experience entered nests more quickly than experienced ones, after controlling for other factors affecting latency, such as the sex, offspring quality and the order of capture relative to the other pair member. Birds' reluctance to enter the nest furthermore increased as the number of captures in previous years accumulated, implying that individual pied flycatchers became progressively more difficult to capture over the course of the study. Our results indicate that repeated exposure to capture stress over an animal's lifetime may induce long-lasting behavioural modifications that may influence trappability of the older segments of the population. We also provide evidence that this may ultimately lead to sampling bias towards younger ages, especially when effort is limited. We conclude that systematic age bias due to trapping experience can have important implications for the estimation of variation in a range of traits and should therefore be carefully checked in longitudinal studies.

Keywords: age, behavioural syndromes, capture–mark–recapture experience, *Ficedula hypoleuca*, parental care, recapture rates, trappability, sampling biases

41 *The standard stress is simply capture, handling, and restraint—it is assumed that all*
 42 *individuals of all species will regard capture and handling as stressful. (Dawson, 2004)*
 43

44 Long-term monitoring of marked animals is usually required for the estimation
 45 of life history and demographic parameters (Stearns 1992; Potti et al. 2013; Sergio et al.
 46 2014). Longitudinal individual-based data are generally obtained by capture–mark–
 47 recapture methods. For this, each animal is marked when captured for the first time and
 48 then recaptured for identification on subsequent sampling. Currently, the development
 49 of modern, but usually expensive, electronic devices allows telemetry monitoring of
 50 individuals with minimal disturbance (e.g. Sergio et al. 2014). However, due to their
 51 low cost and easy deployment, conventional markings (e.g. tags, clips, rings, etc.)
 52 continue to be widely used in field studies (Tyrrell et al. 2009; Kukalová et al. 2013;
 53 Brommer et al. 2015), even when most of them do not allow individual recognition
 54 from a distance, and, therefore, animals need to be recaptured.

55 Field studies on individually marked animals typically rely on traps as the
 56 capture technique because of their proven efficiency, affordable price and safety
 57 (Bateman 1979). Traps, in any of their modalities (e.g. box-traps, drive-traps, corral-
 58 traps, decoy-traps, funnel-traps, spring-traps, etc.) have proven to be an efficient method
 59 for capturing almost any vertebrate organism, including fish (Wilson et al. 2011; Myles-
 60 Gonzalez 2016), reptiles (Tyrrell et al. 2009; Carter et al. 2012), passerine (Friedman et
 61 al. 2008; Garamszegi et al. 2009) and nonpasserine (Heidinger et al. 2010; Brommer et
 62 al. 2015) birds and small to medium-size mammals (Tuytens et al. 1999; King et al.
 63 2003; Kukalová et al. 2013). However, even when the trapping systems may be adapted
 64 to the target species to maximize the capture efficiency while ensuring animal welfare,
 65 the capturing, marking and handling process is not without negative effects.

In many cases, trap shyness, capture stress and neophobia are difficult to avoid when studying animals in the wild (Sutherland et al. 2004; Friedman et al. 2008). For operative and practical reasons, the consequences of those additive and potentially interacting stressors on the ensuing behaviour of individuals are assumed to be negligible, let alone mentioned, in most medium- to long-term population studies (e.g. chapters in Clutton-Brock (1989) and Newton (1989)), including some by the authors of this article (Potti et al. 2013; Camacho et al. 2016). However, an increasing number of studies in ecology and conservation biology highlight the importance of understanding how disturbances caused by researchers affect individual behaviour and trappability of animals (Tuytens et al. 1999; Beale & Monaghan 2004; Biro & Dingemanse 2009; Kukalová et al. 2013; Ibáñez-Alamo et al. 2012; Roche et al. 2013; Merrick & Koprowski 2017), as they may even affect the phenotypic composition of populations (Arroyo et al. 2017).

In wild populations, most of the work on the behavioural determinants and consequences of trappability have been made in avian models (Domènech & Senar 1997; Garamszegi et al. 2009; Mills & Faure 2000; but see also Kukalová et al. 2013; Myles-Gonzalez 2016), although the issues apply to other vertebrates (e.g. mammals, Tuytens et al. 1999; King et al. 2003; reptiles, Carter et al. 2012; fish: Wilson et al. 2011). It is known that songbirds other than those in the Corvidae and Paridae clades, well known for their spatial memory of food stores (Shettleworth 1990; reviewed by Feeney et al. 2009), are able to recognize and respond to stimuli they had previously experienced, both in the medium (song playback recognition; Rivera-Gutiérrez et al. 2015) and the long term (neighbour recognition; Godard 1991). Long-term recognition of trapping devices could obviously affect an individual's trappability in subsequent years, as is often the case in long-term studies where specific successful protocols tend

to be highly conserved (Garamszegi et al. 2009; C. Camacho, D. Canal & J. Potti, personal observation). For example, individuals developing a long-lasting aversion to the traps and human manipulation after being captured for the first time may be more difficult to recapture in subsequent years, and, consequently, data on the older segments of the population might be underrepresented for reasons other than the normal scarcity of old individuals in wild populations (Nisbet 2001; Ricklefs & Scheuerlein 2001; Brunet-Rossinni & Austad 2006; Roche et al. 2013).

Surprisingly, to our knowledge, only one long-term field study (Roche et al. 2013) has directly addressed the implications of being trapped and handled, such as trap aversion underlain by medium- to long-term memory, implicit in Dawson's statement heading this article (but see Elder & Zimmermann (1983) and Senar et al. (1997, 1999) for similar approaches in other contexts). In fact, except for a few recent avian studies spanning relatively short time frames (one to four seasons; Garamszegi et al. 2008; 2009; Linhart et al. 2012; Rivera-Gutiérrez et al. 2015), little is known about the issue of trappability of wild individuals across extended time periods (i.e. spanning at least the life span of a cohort). Such an approach is necessary to understand how trappability varies during ontogeny, which has usually been treated as a nuisance to control for and only indirectly estimated with statistical methodologies, mainly capture–mark–recapture methods (Buckland & Hereward 1982; Elder & Zimmerman 1983; Nichols et al. 1984; Garamszegi et al. 2009; Tyrrell et al. 2009; Roche et al. 2013).

Here, we used the pied flycatcher, *Ficedula hypoleuca*, as a model organism to investigate one component of the behavioural response of target individuals to the risky situation (Frid & Drill 2002; Linhart et al. 2012) posed by a trapping device installed inside their nest, a common method used in nestbox studies where breeding adults are routinely caught for identification, ageing and measurement (Garamszegi et al. 2008,

2009; Camacho et al. 2013; Brommer et al. 2015). This device consists of a swing-trap like that described in Friedman et al. (2008) that allows parents to see and hear their chicks without sensorial obstruction. By following individuals with long capture histories (1–8 successive years), we examined the association between capture experience and individual trappability, measured as latency to enter the nestbox. More specifically, we predicted (1) that ‘naïve’ individuals would have shorter latencies to enter the nest than previously captured individuals; (2) that repeated trapping would have a lifelong effect on individual trappability (e.g. by habituation or long-term memory) and, as a result, the older segments of the population might be assigned different trappability; and (3) that variation in trappability might result in age-biased samples, in which the older segment of the population might be consistently underrepresented. The results of this study will shed light on potential biases that should be considered in long-term studies where assessment of identity and an individual’s life history traits depends on successful, repeated trapping events across its lifetime.

<H1>METHODS

Latency data used in this study were collected during the breeding seasons of 2009 - 2014 as part of a long-term nestbox study of pied flycatchers in central Spain (e.g. Canal et al. 2012; Potti et al. 2013; Camacho et al. 2013; 2016). Pied flycatchers are migrant, obligate hole-nesters with a mainly monogamous mating system, although a variable percentage of males (<25%; Lundberg and Alatalo; 1992) engage in socially bigamous relationships. Both sexes feed the nestlings, although bigamous males often provide less assistance to secondary than to primary females (Lundberg and Alatalo 1992). Our nestboxes are placed on branches 2–5 m above the ground in an oak wood

and an adjacent pine plantation and have been in the same trees since 1988 (pine wood) or 1995 (oak wood; see Camacho et al. 2013 for details of the study site).

In all years, intensive efforts were made by field workers to capture and mark all the breeding population and ring all surviving nestlings near to fledging. All persons operating the traps had > 1 year working experience with the population and had been previously instructed by qualified personnel (C.C. and J.P.). Breeding males and females were captured when nestlings were 8–10 days old (hatching date = day 1) by using a passive, aluminium swing-trap placed inside their nestbox, by which the birds were automatically caught when entering the nest to feed their chicks (Friedman et al. 2008). Parents could see and hear their chicks from the nestbox entrance without hindrance. Note that only one bird per trapping attempt could be captured, because the spring-loaded door of the trap remained closed after one of the members of the pair entered the nest.

Birds present on their territory at the time the trap was set generally moved away and witnessed the observer manipulating the nestbox from afar. However, as soon as the observer retreated, they approached the entrance and looked inside, almost certainly detecting the trap. Most individuals were initially wary and flew away from the nestbox, but soon returned and tried to enter the nest and feed their chicks. Latency to enter could then reflect birds' reaction to both human manipulation of their nestbox and the presence of a novel object inside the nest (Garamszegi et al. 2009). Note, however, that this study aimed to test the effect of exposure to capture episodes as a whole on capture latency, but not to tease apart the effects of the different stressful situations faced by birds during capture.

Field workers hid 20–40 m from the nestbox immediately after the trap was set and recorded the time, to the nearest minute, until the bird finally entered its nest and

the trap closed, that is, the latency to enter the nest ('latency' henceforth). After placing the bird in a cloth bag for posterior data processing, the trap was deployed again to catch the remaining member of the pair and the timer reset to zero. Captured individuals were marked with numbered metal rings and measured for a set of morphological and sexual traits used in other ongoing studies (e.g. Canal et al. 2011; Camacho et al. 2016). The age of previously unmarked birds was estimated following the criteria of Karlsson et al. (1986), although we knew the age of numerous birds marked as nestlings due to high natal philopatry (Potti and Montalvo 1991). Birds were released immediately after being processed, which typically took no longer than 15 min. In most cases, they returned to the nest after their mate had already been caught and the trap removed; thereby normality could be rapidly restored in the nest.

Some individuals were extremely trap-shy and we were unable to catch them within a reasonable time. Because of concerns for the welfare of nestlings (see Götmark 1992), we truncated the capture time at 60 min per session. Nest abandonment the day after the parents were trapped, conservatively assumed to result from manipulation, was only noted in two of 951 nests, suggesting that 60 min trials do not pose a major risk to offspring. For parents reluctant to enter the nest within this period (2%), no additional capture attempts were made on the same day. However, given the valuable information that extreme phenotypes may provide, we made every effort to capture them on the following day(s). Generally, trap-shy individuals were captured by means of an observer-operated trap or by mist netting on the day after the first capture attempt, yet in some cases, two or three additional attempts had to be made. Our sample therefore consisted of some birds caught within the first 60 min trials and some caught after the first trial (24 of 1279 capture attempts), although the latter were excluded from the latency analyses. Birds needing several capture attempts, usually old birds already

trapped in previous years (median (Q1, Q3); captured at first trials: 2 years (2, 3) captured after first trials: 2.5 years (2, 4)), were, however, used to illustrate potential trappability-related biases. For birds that were caught before 2009 the total number of captures exceeded the 6-year duration of this study.

In all nests, we recorded the number of chicks the adults were attending when they were captured, and measured their tarsus length and body mass on day 13 (hatching date = day 1), 3–5 days after adults were captured (Camacho et al. 2016). We limited analyses to records of confirmed socially monogamous pairs.

<H2>Data analyses

To investigate the effect of capture experience on trappability, we ran a geralized linear mixed model (GLMM, normal error distribution, identity link function) with log-transformed latency as the response variable. Capture experience and adult age are largely, but not fully, interchangeable in our study population due to the large variation in the age of first reproduction (1–3 years; Potti & Montalvo 1991). Given that individual experience, in the broad sense, may also influence trappability, controlling for its potentially confounding effects is necessary (Garamszegi et al. 2008; 2009). For this, we took the residuals from the regression of the number of captures on adult age ($F_{1, 1277} = 3913.7$, $P < 0.001$; slope $\pm$ SE = 0.764 ± 0.012 ; $R^2 = 0.75$) and included them in the GLMM as a covariate. Hereafter, we refer to the number of capture events corrected by age simply as ‘capture experience’.

Latency to enter the nest may also be influenced by factors other than capture experience that might potentially confound our results. Birds that had witnessed the capture of their mate before being captured might be more wary of the trap and therefore delay their entry into the nestbox (Friedman et al. 2008). To control for the

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effect of indirect exposure to capture trials on latency, the order of entry of the target bird relative to the other pair member was included in the model as a fixed effect. Moreover, it is known that parents generally take greater risks for larger broods or better-quality offspring, and that the level of risk taking may differ between males and females according to the offspring reproductive value (Michl et al. 2000; Westneat et al. 2011). Mean brood body condition was calculated as the average of the residuals of the regression of fledglings' body masses on their tarsus length on day 13, and then included in the model along with its interaction with sex of the focal parent to account for parents' motivation to enter the nest (Michl et al. 2000). Brood size of pied flycatchers was negatively related to nestling condition (GLMM: $F_{1, 685} = 22.12$, $P < 0.001$; estimate $\pm$ SE = -0.131 ± 0.028) and therefore excluded from the model because of collinearity concerns.

In the GLMM, individual identity was fitted as a random factor to account for repeated measures of the same individuals and for individual variation in feeding rates potentially influencing latency to enter the nestbox. Further, to test for within-individual changes in latency we considered the effects of random slope for capture experience as well as those of the covariance between the slopes and intercepts (Dingemanse et al. 2010; Martin et al. 2011). In this analysis, we also included individuals with only one measure since, on the one hand, they can improve the power to detect between-individual variance in plasticity and, on the other, they might be a nonrandom sample of the population (Martin et al. 2011). However, because our data set contains a large number of individuals captured only once in relation to birds captured more than twice, a model including all individuals regardless of their capture histories did not converge. To avoid convergence problems, a subsample of individuals captured only once was randomly selected to equal the number of individuals captured more than once. Prior to

analyses, we centred individual capture experience on its mean (Dingemanse et al. 2010).

Model selection was carried out by stepwise removal of the random elements from the model while keeping the main effects and interactions. We tested the effect of the random elements with a chi-square likelihood ratio test comparing models including and excluding the focal terms. We began with a random effects structure allowing for random intercepts, random slopes, and a correlation between them. However, neither the correlation component ($\chi^2_1 = 0.07$, $P = 0.79$) nor the random slope ($\chi^2_2 = 2.16$, $P = 0.14$) were significant and were therefore removed from the final model (i.e. the model comprising only the random intercept). Because the random slope component was removed from the final model, all individuals, regardless of the number of captures, were considered to examine the effect of capture experience on latency.

Year was included in the model as a random effect to account for temporal heterogeneity in environmental conditions. Nestbox identity was also included in the model as a random effect to account for unmeasured habitat variation. Latency to enter the nestbox was measured not from when the target bird approached the nestbox entrance and possibly discovered the trap from the outside, but from when the trap was installed, regardless of whether either pair member was present or not (Garamszegi et al. 2009). Because areas of different quality may provide different foraging opportunities for parents, thus influencing their nest visit rates, latency could have been overestimated especially in poor territories, where parents might take longer to find food. In any case, we are confident about our sampling protocol, since there is no reason to think that uncertainty due to unmeasured habitat variation would be heterogeneous regarding the capture experience of individuals.

Before interpreting the output of the GLMMs, we systematically performed model diagnostics statistics to avoid misleading conclusions based on statistical artefacts. To this end, we checked assumptions about the distribution of residuals through diagnostics plots and examined collinearity or the presence of influential cases. These analyses did not show any obvious deviation from GLMM assumptions or any collinearity problems. All analyses were performed in R 3.3.1 ([http://wwwR-project.org](http://www.R-project.org)). GLMMs were fitted using the package 'lmerTest' (Kuznetsova et al. 2016). Model selection of the main effects and interactions was carried out using likelihood ratio tests, as described above. Means are given $\pm$ 1 SE.

<H2>Simulated effects of varying trapping effort

If annual trapping influences pied flycatcher trappability in subsequent years, then it might be expected that insufficient trapping effort would lead to underrepresentation of older and more experienced individuals relative to younger ones. To understand the potential implications of this bias, we simulated the effects of sampling at increasingly longer time intervals by splitting the entire data set into increasing 15 min intervals, thus creating four subsamples of the individuals that would have been caught after 15, 30, 45 and 60 min trapping efforts. Based on this simulation, we examined changes in the mean and variance of bird age in relation to the duration of the trapping session.

<H2>Ethical note

All work was subject to review by the ethical committees at the Doñana Biological Station and the CSIC headquarters (Spain) and adhered to Spain standard requirements.

Birds were caught and ringed under licences from the Ringing Office of the Spanish Ministry of Agriculture, Food, Fisheries and Environment.

RESULTS

We collected data on the latency of pied flycatchers to enter their nests on 1279 occasions (618 male, 661 female), of which we had repeated (between-years) measures for 307 individuals (163 females, 144 males). Birds were caught, on average, on 1.9 ± 0.03 occasions/year (range 1–8). Latency averaged 10.4 ± 0.4 min and 11.1 ± 0.5 min, for females and males, respectively (first and subsequent captures combined). There was no overall trend for either sex to be the first to enter the nest, as males and females did so on 51% and 50% of occasions, respectively ($N = 242$).

Of the target individuals 80% entered the nest within 15 min from trap installation, and 98% did so within the first 60 min trial, indicating that our sampling effort was adequate to capture almost all individuals in the population. Latency increased the more times (years) a bird had been captured, suggesting that previous individual experience in very similar contexts (separated by approximately 1 year) significantly influenced individual trappability (Table 1, Fig. 1).

Birds took longer to enter the nest when their pair mate had already been captured (Table 1), showing that the order of entry could potentially confound our results. However, a GLMM using only birds that had been captured prior to their mates ($N = 681$) confirmed the positive relationship between latency and capture experience (estimate $\pm$ SE = 0.067 ± 0.026 , $P = 0.009$), indicating that the long-term effect of capture experience on latency was independent of that of the order of entry. In addition, fledgling condition significantly influenced latency, although this effect depended on the sex of the parent. Females took less time than males to enter the nest when they

were caring for offspring of higher quality (Table 1), although the significant effect of trapping experience on latency still remained after offspring quality was accounted for.

<H2>Simulated effects of varying trapping effort

When we split the data set into increasing 15 min intervals, we found strong support for the biasing effects of long-term behavioural changes caused by trapping experience. The mean age of all captured individuals was 2.7 ± 0.04 years (range 1–9) but, as shown in Fig. 2, the sample mean increased $+0.03$ years for every 15 min increase in the trapping effort. In addition, the variance of the sample mean, assumed to decrease inversely with the number of samples, remained unchanged at $SE = 0.04$ from the 15 min to the 180 min session despite an overall 20% increase ($N = 267$ birds) in the sample size (Fig. 2), implying that sampling at increasingly longer sessions was nonrandom with respect to individual age. Note that, although the effect of trapping effort on the sample mean was not very pronounced, it clearly indicates that insufficient effort may consistently bias the age distribution towards younger ages due to the increased difficulty of capturing older individuals.

<H1>DISCUSSION

By following pied flycatchers with long capture histories, we have provided evidence that capture experience influenced individual trappability in subsequent years. Birds with previous experience of being trapped and handled by researchers took longer to enter the traps than those captured for the first time, independent of other relevant factors, such as offspring quality or capture order relative to the pair mate. Moreover, they became progressively more difficult to recapture over their lifetime, indicating that repeated trapping may result in long-lasting, increasing aversion to the traps in the pied flycatcher. Possibly, this could apply to other vertebrates as well.

Because of the individual-based nature of our long-term study, we made every effort to capture all pied flycatchers breeding in our nestboxes, which may induce long-term changes in behaviour, as shown here. Most birds that approached the nestboxes to feed young noticed that the trap was installed and perched at the entrance, but did not enter immediately, possibly because the trap forced them to face an apparently inert ‘novel’ (sensu Greenberg & Mettke-Hofmann 2001, i.e. that which is both new and surprising) object inside the nest. Moreover, our trapping procedure certainly posed the dilemma for parents of confronting a possible (for inexperienced birds) or a confirmed (if remembered from previous experience) risk against the fitness benefits of attending their offspring (Dale 1996; Michl et al. 2000). But given that we managed to catch almost all targeted individuals (98%) within a reasonable time (60 min) regardless of their trapping experience, it seems that, after sufficient time has been given to the birds, the stimulus/urgency to feed their offspring overcomes trap aversion.

However, there are some qualifiers to this generalization. Females caring for nestlings that were in prime body condition were more likely than males to overcome trap aversion quickly, as also noted by Dale et al. (1996) in an experimental study in a Norwegian population of the species. The stronger association between risk taking and offspring quality among females might reflect sex-specific differences in confidence of paternity (Michl et al. 2000), since extrapair fertilizations are common in this population (Canal et al. 2011; 2012) and intraspecific nest parasitism does not occur (Dale et al. 1996; Canal et al. 2011; 2012), although a range of environmental and social factors, such as the partner’s behaviour could also be involved (see Westneat 2011).

Latency to enter the nest was also influenced by the relative trapping order of pair members. Indeed, irrespective of sex, the second individual significantly delayed its entrance to the nest after witnessing the capture of its mate or perceiving its absence

(Friedman et al. 2008). This finding suggests that pied flycatchers may be able to anticipate risk in the short term based exclusively on indirect exposure to frightening situations and concurs with other studies showing that seeing attacks by predators often elicits antipredator behaviours in birds (reviewed by Jones et al. 2016).

<H2>Implications of experience-related bias in trappability

Numerous studies have shown that sampling bias due to individual differences in trappability can have important implications for the estimation of life history parameters (Domènech & Senar 1997; Biro & Dingemanse 2009; Garamszegi et al. 2009; Linhart et al. 2012; Roche et al. 2013; Stuber et al. 2013). Here we have shown that the effect of repeated trapping during ontogeny can cause additional bias, which may have important implications for the design of capturing protocols. By splitting the whole sample to simulate the effects of varying effort, we showed that sampling at increasingly longer time intervals was nonrandom with respect to individual age, primarily because we had lower success at trapping old birds in short sessions and, therefore, the right tail of the age distribution was generally missing. Consequently, the age structure of the simulated samples varied according to the duration of the trapping session. Although the age bias due to capture experience in our study might seem small, it should be emphasized that the pied flycatcher has long been a very popular model in evolutionary and behavioural studies due to its high tolerance to nest manipulation, capture and handling. It is therefore possible that the effects of repeated trapping on pied flycatchers are relatively small compared with the effects on other less tolerant organisms, but this remains to be evaluated. Moreover, although a lower success at trapping old birds might not have a dramatic effect on mean age estimates, the right tail of the age distribution might be missed in less tolerant animals, especially if the field protocols are not periodically

revisited and readjusted accordingly (e.g. by comparing estimates obtained through passive and active trapping methods; see Michelangeli et al. 2016).

It is obvious that the implications of these findings may be critical for assessing the variation of any trait among the plethora of those subject to changes during ontogeny, such as timing of breeding (Perrins 1970), reproductive rates (Clutton-Brock & Vincent 1991), variation in parental investment (Stearns 1992) and sexual ornamentation (Badyaev & Duckworth 2003; Saino et al. 2003), to name a few. In wild populations, the older age classes are naturally scarce, which already imposes severe limits on sample sizes. Clearly, this constraint is further aggravated if the older and more experienced individuals become progressively more wary, thus less trappable, when exposed to routine activities of researchers (Arroyo et al. 2017). Trap filtering with increasing age and experience may be a particularly thorny issue for researchers interested in the precision of survival estimates and mortality rates (Nichols et al. 1984) and those looking for evidence of senescence in life history and other ecologically important traits (Hendry & Berg 1999; Møller et al. 2005; Torres & Velando 2007; Péron et al. 2010; Potti et al. 2013).

Likewise, the implications of sampling bias due to trap aversion or, more rarely, attraction to traps (Nichols et al. 1984) may be critical when personality syndromes are investigated. Numerous studies show that passive trapping methods may systematically collect a nonrandom sample of personality types (Biro & Dingemanse 2009; Carter et al. 2012; Biro 2013; Stuber et al. 2013). Garamszegi et al. (2009), who used a nestbox trap similar to ours, showed experimentally that trappability of their study species, the closely related collared flycatcher, *Ficedula albicollis*, was associated with exploration, aggression and risk taking, and included ‘trappability’ in a behavioural syndrome. Other authors have even used trappability as an index of boldness, based on the assumption

that shy animals would be less likely to enter a trap than risk-takers or explorative individuals (reviewed by Michelangeli et al. 2016).

We suggest, however, that the generality of this assumption should be reconsidered in the light of the new findings that repeated trapping (Roche et al. 2013; this study) and exposure to humans (Arroyo et al. 2017) may induce long-lasting behavioural modifications. For example, an inherently bold individual could be misclassified as shy based exclusively on latency scores since, as shown here, its trappability might be determined by past capture history (Dingemanse et al. 2010). Future studies should explore whether inherently shy and bold individuals respond differently to previous capture experience to avoid misleading results.

To conclude, our results indicate that repeated trapping over an individual's lifetime may induce long-lasting behavioural modifications that may ultimately influence its trappability on subsequent sampling, with important implications for the accurate assessment of life history parameters. We conclude that many ecological and behavioural studies based on capture–recapture data would benefit from a greater understanding of the factors influencing individual trappability in the long term. We recommend researchers to retrospectively investigate the issue with their data at hand to make sure that their field and capturing protocols do not result in unwanted loss of valuable biological information on the older segments of their study populations.

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627 Table 1. Results of the GLMM model explaining the variation in latency of adult pied
 628 flycatchers to enter their nest equipped with trapping gear

	Estimate	SE	<i>df</i>	<i>t</i>	<i>P</i>
Intercept	1.02	0.14	18.68	7.19	<0.001
Capture experience	0.09	0.04	1120.20	2.26	0.024
Capture order	0.66	0.05	969.34	13.93	<0.001
Sex	0.00	0.05	934.05	0.07	0.940
Nestling condition	0.27	0.09	956.40	2.95	0.003
Sex*nestling condition	-0.12	0.06	926.18	-2.13	0.034

Number of observations = 1131; number of individuals = 777; number of nests = 268;
 number of years = 6.

629 **Legends to the Figures**

630

631 **Figure 1.** Relationship between latency to enter the nestbox trap and capture experience
632 in previous years (number of annual captures corrected by age) in breeding pied
633 flycatchers. The line shows the values predicted by the GLMM.

634 **Figure 2.** Trappability bias as a function of the age of pied flycatcher parents. The mean
635 $\pm$ SE ages of trapped, adult pied flycatchers are shown in relation to the duration of the
636 trapping session. Numbers beside bars are (accumulated) numbers of birds.