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# Paradoxical associations between fitness components and behavioural phenotype in a wild bird



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#### ARTICLE INFO

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Keywords: behavioural syndrome Lincoln's sparrow Melospiza lincolnii neophobia reproductive success trappability Individually consistent behavioural phenotypes persist in a diversity of populations, despite the expectation that selection would reduce their prevalence. The life-history trade-off between current and future reproduction, combined with individual variation in age or condition and therefore in residual reproductive value, may explain this apparent paradox. Specifically, individuals that are old or of low condition and therefore of low residual reproductive value should take risks and thus elevate current reproduction at the expense of future reproduction. The opposite should be true for individuals that are young or of high condition and therefore of high residual reproductive value, which should be risk averse. Over the course of a long-term study on Lincoln's sparrows, Melospiza lincolnii, we discovered a behavioural phenotype based on trappability that predicts both condition (but not age) and current reproductive success but, surprisingly, in a way that was not expected based on our assumption of how this phenotype is associated with risk taking. We found that, relative to individuals that did not enter traps (the nontrap phenotype, assumed as risk averse), those of the trap phenotype (assumed as risk taking) showed elevated indices of energetic condition and, for females, reduced reproductive success. Assortative mating may be a proximate mechanism for the populationwide maintenance of multiple behavioural phenotypes, and we found that assortative pairings based on trappability phenotype occurred more frequently than random pairing would predict. However, assortative pairing, when compared to disassortative pairing, did not affect reproductive success. Nevertheless, the contrasting relationships between current reproductive success and condition that we found for each phenotype are consistent with life-history theory. However, our results are not consistent with the assumption that the trap phenotype is a manifestation of risk-taking behaviour and may, in fact, arise from just the opposite: a risk-averse, shy or neophobic behaviour for the trap phenotype.

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Consistent, within species, between-individual variation in behavioural phenotype is common (Dall et al., 2004; Sih et al., 2004; Wilson et al., 1994), despite evidence for the heritable, genetic basis of such variation (Drent et al., 2003; Henderson, 1986; Sluyter et al., 1995; van Oers et al., 2004; Weiss et al., 2000) and the tendency of selection (e.g. Réale & Festa-Bianchet, 2003) to reduce it. The life-history trade-off between current and future reproduction (Williams, 1966) could explain this apparent paradox, in that individual variation in age- or condition-dependent reproductive value may affect how selection acts on behavioural phenotype (Clark, 1994; Wolf et al., 2007). Specifically, in old or low-condition individuals, whose prospects for future reproduction are low, selection should promote bold, risk-taking behaviour that facilitates current reproduction. Conversely, in young or high-condition individuals, whose prospects for future reproduction are high, selection should promote shy, cautious behaviour that favours survival over current reproduction (Cole & Quinn, 2014; Smith & Blumstein, 2008). Variation in age or condition, together with the life-history trade-off between current and future reproduction, could thus drive selection for variation in behavioural phenotype.

Several studies have shown that behavioural phenotype is associated with various fitness components, including attractiveness to a prospective mate (Godin & Dugatkin, 1996), the strength and formation latency of pair bonds (Firth et al., 2018), mating success (Reaney & Backwell, 2007), reproductive success (Both et al., 2005; Dingemanse et al., 2004; Mutzel et al., 2013; Réale et al., 2009), and extrapair paternity (Patrick et al., 2012). Sometimes these associations arise through complex, multifactormediating mechanisms (Mutzel et al., 2013). Insofar as any of

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these fitness components may trade off with others, such as survival (Dingemanse et al., 2004; Dingemanse & Réale, 2005; Réale & Festa-Bianchet, 2003), selection may favour the persistence of multiple behavioural phenotypes in a population that varies in age or condition, as explained above. Nevertheless, behavioural phenotype may not necessarily be associated with either age or condition (Dingemanse et al., 2002; Dingemanse & Réale, 2005), suggesting the need to better understand the relationships between behavioural phenotype and fitness components in a diversity of natural populations, each of which may vary in its own natural history and thus in the way behavioural phenotype affects fitness.

From a long-term study on Lincoln's sparrows, *Melospiza lincolnii*, we have discovered that some individuals enter seed-baited traps, whereas others do not (see Results). In some systems, such trappability, when defined less restrictively than we did (see below), may not be a proxy for behavioural phenotype, depending on whether other factors, such as spatial, temporal and sex- and age-based variation play a role (Brehm & Mortelliti, 2018). We largely rule out these other factors (see Results) and more restrictively interpret trappability in our study as a dichotomous behavioural phenotype that is unchanging in the individual (trap versus nontrap).

Exactly how the trappability phenotype may arise is not clear, but some evidence suggests it may be related to exploratory, risktaking or neophilic behaviour. Since Audubon and Bowen's (1841) description of this species 183 years ago, the Lincoln's sparrow has been known for its furtive and elusive behaviour, even among birds (Ammon, 2020; Roberts, 1932; Speirs & Speirs, 1968). Philopatry is very low in our study population (ca. 4% of fledglings return in a subsequent year as adults) (Sockman, 2012), and to our knowledge, there are no locations elsewhere at which fledgling or adult Lincoln's sparrows are likely to have encountered traps before dispersing to our site. This and the fact that the traps are made from a metal wire mesh and with uniform, geometrical shaping strongly suggest that the traps appear as novel objects to the adult subjects of our study when they encounter them for the first time in their lives, as adults on our site. We therefore assume that variation in the trappability phenotype is a manifestation of variation in risk aversion, neophobia or exploratory behaviour, as others have proposed for trappability in a variety of systems (Biro & Dingemanse, 2008; Carter et al., 2012; Réale et al., 2000; Wilson et al., 1993), but confirmation of this assumption awaits the determination of whether or not the two phenotypes show a similar difference in approach towards other novel objects but no such difference in approach towards familiar objects.

This incidental discovery of a behavioural phenotype, in combination with a data set on several fitness components, presented an opportunity to examine how behavioural phenotype is associated with fitness components in a wild, free-ranging organism and whether the relationships between phenotype and fitness components are consistent with the predictions based on the lifehistory theory described above. Hypothesizing that use of traps derives from risk-taking, neophilic or exploratory behaviour, we predicted that the trap phenotype, when compared to the nontrap phenotype, is of lower condition and thus elevates reproductive effort and reproductive success. We also predicted that the probability of the trap phenotype increases as the individual ages due to the decline in residual reproductive value with age. In previous work, we determined that the trap seed does not constitute a significant portion of the birds' diets (Beaulieu & Sockman, 2014), and the seed, therefore, is unlikely to contribute directly to phenotypic differences in condition.

Studies on the relationship between behavioural phenotype and reproductive success raise questions regarding the prevalence of assortative (or disassortative) mating (Schuett et al., 2010) on the character or characters that define the phenotype. Assortative mating may be a proximate mechanism for the populationwide maintenance of individual variation in phenotype (Kralj-Fišer et al., 2013) and itself may be proximately driven by a high probability of encountering a mate of similar phenotype, as may be expected for phenotypes that are based on exploratory behaviour, risk aversion and neophobia. Alternatively, assortative mating may be proximately driven by mating preferences for traits correlated with the phenotype. Ultimately, selection to maximize genetic compatibility could favour mating preferences for either the same phenotype (e.g. genetic similarity) or a different phenotype (e.g. heterozygote advantage) (Schuett et al., 2010). Furthermore, an individual might benefit from choosing a mate of similar phenotype (Both et al., 2005; Harris & Siefferman, 2014) because the pair might better coordinate parental and other forms of reproductive activity in ways that enhance reproductive success (Schuett et al., 2010). However, in some situations, although assortative mating may enhance current reproductive success, it may reduce fitness compared to disassortative mating (Dingemanse et al., 2004; Dingemanse & Réale, 2005), and thus disassortative mating could be favoured in the long term. In short, the question of whether behavioural phenotypes mate assortatively has important implications for the proximate maintenance of behavioural phenotypes in a population, and thus we also examined its prevalence in this present study.



**Figure 1.** (a) Two-cell trap used to capture Lincoln's sparrows and define trap and nontrap phenotypes. (b) Traps were baited with raw millet seed and placed under the canopy of small willows (*S. glauca* or *S. wolfi*). Twigs were used to prop open the trap doors, allowing birds to enter and exit during nontrapping periods. During trapping periods, twigs were removed and the tripping mechanism was set by sliding the arm connected to the treadle beneath each door (left cell in (a)), such that the weight of a bird depressed the treadle, causing the door to fall and the individual to be captured.

# METHODS

#### Study Site and Species

This study used data collected in June and July of 2005–2016. except in 2014, all from a single, ca. 15 ha study site near Molas Pass. Colorado (U.S.A.) at 37.74°N, 107.69°W and 3200 m elevation. We have described details of this site previously (Beaulieu & Sockman, 2012a; Sockman, 2008, 2009). Briefly, it is a subalpine, open-field habitat dominated by shrubby willows (Salix glauca and Salix wolfii) and sedgy (Carex nebrascensis) clearings characteristic of the habitat of Lincoln's sparrows, which breed at high-elevation or high-latitude wet meadows in the U.S.A. and Canada, from approximately 34° to over 64° North latitude (Ammon, 2020). According to citizen science observations (eBird, 2017), Lincoln's sparrows overwinter in Central America, Mexico and the southern and far western contiguous U.S., and Molas area individuals arrive from overwintering grounds in May. They lay and incubate eggs and raise nestlings from early June to late July, depending on the pair. Nests are open-cup and built on the ground, usually beneath a small willow. Clutch size ranges from three to five eggs, with a mode of four. Incubation, by the female only, lasts 11–13 days. Nestlings are brooded by the female and fed by both parents for 9-12 days (mean 9.8 days). Fledglings are provisioned for approximately two additional weeks before they gradually gain independence in late July through August, after which all individuals depart for overwintering grounds by the end of September (eBird, 2017).

# Field Procedures

Each breeding season we established a line of seed-baited traps, each uniformly shaped of rigid welded wire (Fig. 1). Each trap was  $36 \times 18 \times 18$  cm, with two cells, one on each side, separated by a rigid wire wall, and with a mechanism on each side that enabled a door to fall closed when the weight of a bird on a treadle tripped it, thus trapping the bird. This style of trap is used widely by field ornithologists (Gaunt et al., 1999) and is often referred to as a Potter trap. We dispersed them throughout the study site and positioned each on the ground beneath the canopy of a willow shrub. In 2005, we established 48 trap locations on the site, altering 15 on one occasion that year. In 2006, we established 70 and altered three locations. From the beginning of the 2007 season, we maintained the same 50 locations each year. We determined all trap locations with a hand-held global positioning system (GPS) unit (Garmin eTrex, Garmin International, Inc., Olathe, KS, U.S.A.).

Traps were positioned and each cell was baited (although not necessarily set for capture; see below) for the first time each year at the end of May or in the first week of June, approximately 2 weeks before peak season for nest initiation (see Results). We baited each cell in the morning with roughly 2 g of raw millet seed with husks and replenished seed daily as needed. One week or less after starting to bait traps any given year, we began setting them for capture for a 2 h period each day. When traps were not set for capture, the door to each cell was propped open, allowing birds to enter, gather any remaining seed, and exit. The vast majority of days across years of the study were nearly identical in terms of trapping effort. Between 0700 and 0800 hours local time each day beginning in early June, we would start to bait and open half the traps, the odd-numbered traps on odd-numbered dates and the evennumbered traps on even-numbered dates. Odd-numbered traps covered the same general extent of the study site as evennumbered traps did. Each trap would remain set to capture for approximately 2 h each day, with one check occurring at approximately 1 h from setting and a second check and unsetting of the trap for the day occurring at approximately 2 h from setting. This was repeated every day for 4–8 weeks, depending on that season's priorities. Thus, for the vast majority of 11 seasons, we assessed each individual that year for the trap phenotype 2 h every morning for approximately 30–50 days.

Despite this abundance of opportunity for any individual bird to find a baited trap and enter it at least once in its lifetime, we routinely observed individuals that did not enter traps, as indicated by their lack of bands (see below). We would even observe unbanded individuals perched directly above or adjacent to a trap sometimes. We captured these individuals by mist net (Gaunt et al., 1999) as follows. After observing the individual's location for 10-20 min, we would string one and occasionally two nets, each 6-12 m long and 2 m high, between two or three of the bird's favoured perch locations. We monitored the net from a distance, typically capturing the bird within 5–15 min of set-up after one of its flights between the locations. If we had not captured the bird after approximately 30–45 min, we would remove the net and try again on another day. However, most netting was successful during the first attempt, and by the end of the season, we rarely observed unbanded individuals on our site.

Once captured, whether by trap or net, we banded individuals with a uniquely numbered aluminium band from the U.S. Geological Service and three coloured plastic bands for subsequent identification from a distance. We determined sex based on a validated (Beaulieu & Sockman, 2014) technique using the presence of a cloacal protuberance (e.g. Morton, 2002) and measured body mass with a 25 g spring-loaded scale. We also scored visible fat deposited subcutaneously in the furcular fossa of each individual. Score values were 0–5, which corresponded to fat that was, respectively, invisible—bulging outward (Wingfield & Farner, 1978). On the first capture of an individual (i.e. when we were also banding it), we used a wing ruler to measure the lengths of the left and right wing chord, ninth primary feather and outer rectrix feather and dial callipers to measure the left and right tarsus (Pyle, 1997).

We previously described details of our nest-finding and nestmonitoring protocols (Sockman, 2008, 2012, 2018). Briefly, we found nests by searching habitat and recorded the location of the nest as we did above for traps or with an application (Pocket Earth Pro, GeoMagik, LLC, Santa Cruz, CA, U.S.A.) running on a mobile phone with a GPS sensor and with various versions of the iOS (Apple, Cupertino, CA, U.S.A.) operating system. All nest checks occurred during daylight hours only, with the vast majority occurring between 0600 and 1600 hours local time. Before and during laying, we checked nests daily to identify the clutch initiation date and clutch size. If we did not know when the clutch was completed (for example, because we had found the nest sometime during incubation), we checked the nest daily to determine when hatching occurred. Nests with a known date of clutch completion and therefore with a predicted date of hatching (based on a typical incubation period) were checked for hatching once or twice daily beginning about 2 days before hatching was expected. Daily checks continued until all eggs hatched (or were deemed nonhatching). For nests found in time, we directly observed the date of clutch initiation, and, for nests found after the first egg was laid, we estimated date of clutch initiation from the clutch size, mean incubation period and mean nestling period.

We identified the parents paired at a nest either by flushing the adults from the nest into a mist net or by observing their colour bands either after flushing from the nest or while they were travelling to and from the nest feeding nestlings or removing faecal sacs.

Each season we also collected audio recordings of male songs (female Lincoln's sparrows do not produce song), as part of other projects on male song communication (e.g. Beaulieu & Sockman, 2012b; Caro et al., 2010; Lyons et al., 2014; Sockman, 2009). We

identified each male being recorded from the unique combination and arrangement of his coloured leg bands, and we also recorded the location of his song perches as described above for nests.

# Ethical Note

The U.S. Department of Agriculture Forest Service (authorization IDs: COL 258, COL 584, COL749), the U.S. Department of the Interior Geological Survey Bird Banding Laboratory (permit number: 23370), the U.S. Fish and Wildlife Service (permit number: MB099926), the Colorado Division of Wildlife (licence numbers: 05-13, 15-16 TRb1056) and the University of North Carolina Institutional Animal Care and Use Committee (IDs: 05-138.0, 08-089.0, 11-090.0, 15-103.0) granted permission for this study.

#### Variable Definitions and Calculations

The number of times an individual was captured in a trap ranged from 0 to 51. Of the individuals that were captured at least once, banded, sexed, measured and released, 40% were never trapped (see Results) and the remaining 60% showed a strongly rightskewed distribution of trapping frequency, with nearly 20% (of the 60%) having been trapped only once. Despite this continuous, between-individual variation in trapping frequency, we defined trap phenotype dichotomously based on whether the individual was ever captured in a trap, even if just once. This variation in trap count among birds that were ever trapped was likely due, in part, to stochastic reasons rather than something more biologically interpretable, such as variation in degree of risk aversion. That is, some individuals would have been found captured in traps very shortly after they had entered them for the first time. These individuals would likely have associated the traps with the punishment of our handling them, rather than the reward of the seed, and never returned to a trap. Others, with longer wait times between trap entry and handling, would have associated the trap with the seed they obliviously consumed rather than the handling they experienced sometimes several days (before traps were first set) following their decision to enter the trap for the first time. This is not to say that variation in trap phenotype was not continuous, but rather that we could not be certain we had a suitable measure to describe that variation. We could be certain, however, that the decision whether or not to enter the trap for the first time was unlikely to have been tied to any stochastically driven association with being handled. Incorrectly classifying this variable as dichotomous or continuous would seemingly increase error but not bias our analyses, meaning that any positive results would be despite, not because of, any error in classification.

For analyses that involved clutch size, we excluded nests found after laying was complete (and that could have lost an egg) and nests that failed before the female completed the clutch. Analyses of hatchling count included only those nests with at least one hatchling and excluded those for which a definitive hatchling count could not be determined, for example if they were depredated during the hatching period. We operationally defined fledgling count as the number of nestlings in the nest when the brood was 7 days old. Although we were not able to confirm fledging with this approach, once a brood fledged, we did not attempt the very difficult, if not impossible, task of relocating and identifying all fledglings. Fledglings almost never entered traps, and their short, infrequent and unpredictable flights made netting any of them, let alone a complete brood, futile. Thus, we could not wait until fledging to estimate fledgling count. As part of other studies, we collected body measures of nestlings, and we usually did so no later than at 7 days of age so as not to trigger premature fledging, which can occur as early as 8 days. Although a few nests for which we determined an operational fledgling count may have failed to fledge (e.g. due to predation after day 7), we assumed that the number was not strongly biased according to the phenotype of the parents. Fledgling counts included only nests with at least one fledgling, as we defined it, and thus excluded abandoned nests and those that were depredated prior to having a 7-day-old brood.

To estimate adult body size, we used the first-axis factor scores from a principal components analysis on the mean (left and right) measure of tarsus, wing chord, primary and rectrix (Sockman, 2009). Body condition was the residual of body mass regressed on body size.

## Statistical Analyses

For statistical analyses, we performed generalized linear and mixed, multilevel modelling with nested or crossed random effects when appropriate (and when possible), using linking functions based on the type of response variable (Stata/IC version 15.1, Statacorp, College Station, TX, U.S.A.), as detailed below. When there was variation between units of a random effect in the value of a model's predictor, we modelled the effect as both a random intercept and a random coefficient for that predictor, as Schielzeth and Forstmeier (2009) showed is necessary. Otherwise, the effect was modelled as a random intercept only.

Sample sizes varied between analyses due to variation in the data that were available for each individual or nest. For example, missing rectrices precluded our estimate of condition for an individual that may have been used for other analyses that did not require rectrices, such as body mass. Similarly, nests for some analyses, such as clutch initiation date, could not be used for others, such as fledgling count, if they did not last until fledging, as we defined it (see above). During several seasons we conducted a manipulative egg substitution experiment on a small subset of nests (Sockman, 2016, 2018). It is possible that procedures associated with this experiment affected hatchling or fledgling count, and thus nests involved in this manipulation were excluded from those analyses. However, the procedures could not have affected nest location or clutch initiation date, and there is no reason to think they could have affected clutch size either. Thus, nests involved in the experiment were not excluded from those analyses.

To determine whether the frequency of the two phenotypes differed by sex, we fitted a logistic regression model with sex as a predictor and, as the response, the dichotomous phenotype, scored as 0 for nontrap and 1 for trap. We then determined whether assortative pairing based on the trap phenotype was more or less likely than random. In monogamous, sexually pairing populations, in which pairing is random and two possible phenotypes are evenly divided by sex (as we found; see Results), the probability of assortative pairing ranges from 0.5, when both phenotypes are equally represented, to 1.0, when only one phenotype is represented. We modelled the probability of assortative pairing with a mixed-effects logit model with no predictors. The mate of both sexes can change between the individual's successive nests, especially between nests of different years, a situation appropriate for crossed (as opposed to nested) random effects (Rabe-Hesketh & Skrondal, 2005). Therefore, in this model, we crossed female identity and male identity as random intercepts. We then converted the intercept of this model (the log odds of the probability) to a probability and compared the 95% confidence interval of the probability of assortative pairing with the probability predicted by the relative frequency of each phenotype observed in our population. We used the same statistical analysis to also model the probability of trap versus nontrap phenotype for assortative pairings only. As an additional approach to examining the extent of assortative pairing, we used a logistic regression with male

phenotype as the response and female phenotype as the predictor, using only nests that were the first known for each male across all years of the study. These were the first nests known to us but not necessarily the first nests of the individuals; some nests, for example, were abandoned shortly after initiation and thus escaped our discovery, as evidenced by the occasional presence of young, unbanded fledglings on the study site.

Behavioural phenotypes, particularly those associated with neophobia or risk aversion, can vary with age of the individual (e.g. Biondi et al., 2010; Greggor et al., 2020). Although we did not know the precise ages of adults in our population, we identified 629 adults for at least one annual breeding season, 302 for at least two seasons, 172 for at least three seasons, 88 for at least four seasons, 48 for at least five seasons, 29 for at least six seasons, 10 for at least seven seasons, 6 for at least eight seasons and 1 adult for nine seasons, yielding an average of approximately 50% annual adult mortality (assuming the probability of identifying an adult does not vary with age). This rate of adult mortality is consistent with other small, migratory songbirds that breed under the climatically challenging conditions of high elevation in the temperate zone (Morton, 2002). We assessed the potential role of age on trap phenotype by analysing whether the probability of being captured in a trap at least once differed between the individual's first year of capture and 1, 2, 3, 4, 5, 6 or 7 years later (although sample size diminished and results became less meaningful with each comparison), using seven similar mixed-effects logit models, with the time span as a dichotomous predictor and with observation nested within individual as a random intercept and a random coefficient for time span. For example, in the first analysis, whether or not the individual was captured in a trap at least once was the dichotomous response and year (first year versus second year) was the dichotomous predictor. The next analysis was the same, except that the predictor contrasted the first with the third year, and so on. Each analysis used only individuals that survived the time span, ensuring that mortality did not drive or obscure between-year differences in trap count.

Next, we determined whether the two phenotypes differed in their temporal distribution and in their spatial distribution relative to the traps. For this, we used the locations of song perches (males only) and nests and a phenological measure, clutch initiation date. We began by calculating the distance from each singing perch to the closest trap at the time of the recording. We often had numerous recordings from an individual male singing from different locations over multiple years. So, we modelled distance as a function of phenotype using a mixed linear model, crossing individual identity as a random intercept with year as a random intercept and as a random coefficient for phenotype.

For the seasonal timing and distance of a nest to the nearest trap, a nest could be associated with both phenotypes if it were owned by two disassortatively paired adults. Disassortative pairings obviously necessitate some degree of spatial and temporal overlap between the two phenotypes. However, most pairings were assortative (see Results), meaning that the two phenotypes could be at least partly segregated in space or time. Additionally, apparent effects of one sex's phenotype on nest attributes and outcomes could be driven by the phenotype of the individual's mate. Therefore, beginning with this assessment of nest distance to the closest trap and continuing for subsequent analyses involving other responses tied to the nest (see below), we modelled the effects of male phenotype simultaneously with that of female phenotype, so that any effect of one sex's phenotype would be controlled for when analysing that of the other sex's phenotype. However, our models of these other nest responses failed to converge while crossing male and female identity as random effects, presumably due to the large number of units for each random effect relative to replicates of that unit in the model. Therefore, we abandoned the mixed-model framework and instead analysed only nests that were the first known over the course of the entire study for both the male and the female, ensuring analyses involved only one nest per individual male and per individual female. This approach substantially reduced our sample sizes but ensured that we did not violate assumptions of independence of the data.

With the above as our framework for analysing nesting outcomes, we then calculated the distance of each nest to the trap that was nearest to the nest 4 days prior to clutch initiation, the approximate time that we estimated nest construction to have begun. Using a general linear model, we fitted male phenotype and female phenotype as predictors (using only nests that were the first known for each sex and therefore no random effects). We did the same for the ordinal date of clutch initiation as a response.

Next, we asked whether phenotype affected our estimates of energetic condition and body size in adults. We tried to minimize the effects of the seed in traps on the estimates of energetic condition by using data from the individual's first capture only, meaning that we used only one observation per individual in these analyses and therefore no random effects. Additionally, for approximately the first 2 weeks each season, we concentrated our efforts on trapping and not mist netting, at which point we usually no longer trapped new, unbanded individuals, despite their presence on the study site (see Field Procedures above). Thus, our mistnetting efforts typically commenced about 2 weeks later than our trapping efforts. This seasonal difference in first capture date could explain apparent differences between the phenotypes in our estimates of energetic condition, so all such analyses included ordinal date of capture as a covariate to control for potential effects of date. The body size measure is assumed not to change either seasonally or over the adult life span; hence, we did not control for date of capture in its analysis, and we measured each individual only one time in this way. Although measuring individuals multiple times could have improved accuracy of these estimates, any measurement error is likely to result in noise variation but not bias with respect to our predictor of interest, phenotype.

In two general linear models, we assessed body mass and body condition as responses, with individual phenotype and ordinal date of capture as predictors. Approximately 75% of fat scores were 0, so we modelled it dichotomously as visible (1) or not (0), using a logistic regression with individual phenotype and ordinal date of capture as predictors. In an additional general linear model, we assessed body size as the response and individual phenotype as the predictor.

The bias towards assortative pairings, combined with significant relationships between phenotype and body mass, condition and visibility of furcular fat (see Results) raised the question of whether individuals paired assortatively based not only on phenotype but more specifically on these correlates of phenotype. Thus, we examined this in four models, using only the first known pairing (nest) of the male, in which the male measure (body mass, condition and presence of furcular fat) was the response and his mate's measure was the predictor, while controlling for date and phenotype of the mate by including them as additional predictors. Analyses used logistic regression for the dichotomous response (presence of furcular fat) and general linear models for the continuous responses (all others).

We assessed the relationship between phenotype and reproductive effort and success in three ordinal logistic regressions corresponding to clutch size, hatchling count and fledgling count as responses and male and female phenotype simultaneously as predictors, using only one nest per individual, the first known over the entire study of both the male and female. Finally, we repeated each of these three analyses but replaced the male and female phenotype predictors with a single predictor, whether (1) or not (0) the pairing at the nest was assortative.

# RESULTS

#### Frequency of Phenotype Based on Sex and of Assortative Pairing

Of 633 sexed individuals (318 females, 315 males), 378 (60%) were of the trap phenotype and 255 (40%) were of the nontrap phenotype. Females and males were evenly distributed between phenotypes (z = -0.02, N = 633 individuals, P > 0.2; Fig. 2).

Our model estimated 67% of pairings as assortative (z = 4.42, N = 326 pairings between 232 females and 205 males, P < 0.001; Fig. 2). Not included within the estimate's 95% confidence interval (60–74%) was the 52% predicted by random pairing and the above-indicated frequency of the two phenotypes and equal distribution of sexes. Our additional approach to assessing assortative pairing yielded similar results, in that the female's phenotype strongly predicted the phenotype of her mate (z = 4.54, N = 205 pairings, P < 0.001).

Although the statistical analysis we used to model the probability of the trap phenotype among only assortative pairings did not converge on a solution, the observed proportion of 68% was nearly identical to the 69% predicted by random pairing and the aboveindicated frequency of the two phenotypes and equal distribution of sexes.

# Age-related Change and Spatial and Temporal Distribution of Phenotypes

We observed no age-related change in the probability of being trapped. The probability of being trapped at least once in the second (N = 302 individuals), third (N = 172 individuals), fourth (N = 88 individuals), fifth (N = 48 individuals), sixth (N = 29



**Figure 2.** (a) Frequency distribution of sex (M, F) with respect to phenotype (nontrap vs. trap) in Lincoln's sparrows. (b) Frequency of disassortative pairings (DP) and assortative pairings (AP) according to the female's phenotype (nontrap vs. trap), and thus her mate's phenotype in Lincoln's sparrows.

individuals), seventh (N = 10 individuals) and eighth (N = 6 individuals) year did not significantly differ from that in the first year (all |z| < 1.06, all P > 0.2).

We examined the relationship between phenotype and the distance from the nearest trap to a male's singing perches, as an indicator of the location of his territory. Nontrap males sang from perches that were an average ( $\pm$  SEM) of 33.7  $\pm$  4.80 m from the nearest trap, whereas trap males sang from perches that were an average of 24.6  $\pm$  4.01 m from the nearest trap, a difference that was not statistically significant (z = -1.45, N = 1612 observations from 178 males over 11 years, P = 0.15; Fig. 3).

Phenotype of the female, but not necessarily the male, was related to the spatial distribution of nests. Of 160 nests that were first known for both the male and female, trap females nested approximately  $5.7 \pm 2.1$  m closer to traps than nontrap females did (z = -2.67, P = 0.008), whereas trap males nested  $3.1 \pm 2.1$  m closer to traps than nontrap males did (z = -1.50, P = 0.14; Fig. 3). The phenological distribution of clutch initiation date (N = 159 nests) was nearly identical between the two phenotypes (female phenotype: z = -1.07, P > 0.2; male phenotype: z = 0.01, P > 0.2; Fig. 3).

# Phenotypic Differences in Measures of Condition and Body Size

Individuals of the trap phenotype were 4.5% heavier (z = 6.29, N = 607 individuals, P < 0.001), of higher body condition (z = 5.10, N = 587 individuals, P < 0.001) and over three times more likely to have visible fat in the furcular fossa (z = 5.26, N = 555 individuals, P < 0.001) than nontrap individuals (Fig. 4). These differences could not be explained by differences in measurement date, which was controlled for in the analyses.

In contrast to these effects of phenotype on our estimates of energetic condition, we observed no relationship between phenotype and body size (z = 0.16, N = 620 individuals, P > 0.2; Fig. 4).

When we controlled for phenotype of the female as a co-factor, none of the female values of the correlates of the phenotype (body mass, condition, probability of furcular fat) significantly predicted the same phenotypic correlates of her mate (all  $z \le 1.0$ , P > 0.2), thereby reflecting no detectable assortative pairing for these traits.

# Phenotypic Differences in Reproductive Effort and Success

We observed no effect of either the female's (z = -0.35, P > 0.2) or male's (z = -1.55, P = 0.12) phenotype on clutch size (N = 68nests) (Fig. 5). However, although phenotype of the male did not appear to affect hatchling count (z = -1.35, P = 0.18), females of the trap phenotype showed lower hatchling counts than nontrap females (z = -2.20, N = 112 nests, P = 0.028; Fig. 5). Similarly, fledgling count appeared unassociated with phenotype of the male (z = 0.44, P > 0.2) but was strongly associated with the phenotype of the female (z = -3.16, P = 0.002), again with fewer fledglings resulting from trap females than from nontrap females (N = 87nests) (Fig. 5). Whether or not the pairing was assortative did not appear to affect clutch size (z = -1.33, N = 68 nests, P = 0.18), hatchling count (z = -1.18, N = 112 nests, P > 0.2) or fledgling count (z = -1.26, N = 87 nests, P > 0.2).

# DISCUSSION

Despite selection's tendency to reduce many betweenindividual differences, individually consistent behavioural phenotypes persist in a diversity of wild populations (Dall et al., 2004; Sih et al., 2004; Wilson et al., 1994). The life-history trade-off between current and future reproduction (Williams, 1966), combined with variation in residual reproductive value, may, in some systems, account for this apparent paradox (Clark, 1994; Wolf et al., 2007).





**Figure 3.** Spatial and temporal distributions of trap and nontrap phenotypes in Lincoln's sparrows. Spatial distributions (circles) were analysed as the distance of (a, b) male singing locations and (c, d) both sexes' nest locations to the nearest trap (crosses). Singing location (first recordings only) and nesting location relative to trap location (a, c) closely mirrored available habitat at the site. (d) Temporal distributions were measured as the date of clutch initiation (square symbols, right axis). Sample sizes (number of nests or singing males) are indicated above points (means  $\pm$  SEM).

Specifically, as residual reproductive value declines with declining condition or increasing age, risk-taking, neophilic and exploratory behaviour should increase, thereby increasing current reproductive effort and success. Here, in a wild, free-ranging songbird, we discovered a behavioural phenotype that predicts both condition and current reproductive success but, surprisingly, in a way that was not expected based on our assumption how the phenotype is associated with risk-taking, neophilic or exploratory behaviour. Relative to females that did not enter traps, females of the trap phenotype, which we predicted would be more risk taking, exploratory or neophilic, had reduced reproductive success and elevated indices of energetic condition. Although our evidence in males for a relationship between phenotype and reproductive success was not strong, males of the trap phenotype, like females, had elevated indices of energetic condition relative to the nontrap phenotype. Assortative pairings occurred more frequently than random pairing would predict. However, we found no evidence that assortative pairing affected reproductive effort or reproductive success. For the most part, sample sizes were large, and thus analyses were powerful for detecting relationships when they existed.

# No Evidence of Age, Spatial or Temporal Dependence of Phenotype

Residual reproductive value is expected to decline with age (Williams, 1966), leading to the prediction that taking risks, exploration, neophilia (Wolf et al., 2007) or, in our study, the probability of trap phenotype, would increase with age. In contrast to this prediction and to other studies on the relationship between age and behavioural phenotype, including one on crows (*Corvus hawaiiensis*) (Greggor et al., 2020) and another on alpine chamois, *Rupicapra rupicapra* (Morin et al., 2016), we found no evidence that phenotype changed in either direction with age. Individuals in their second through eighth adult year were neither more nor less likely to have been captured in a trap at least once than in their first adult year. Our failure to find support for this prediction could be due to the limited life span of the species. With an annual adult mortality



Phenotype

**Figure 4.** Relationship between phenotype and measures of energetic condition (body mass, body condition, proportion of individuals with visible furcular fat) and body size in Lincoln's sparrows. N: nontrap phenotype; T: trap phenotype. The number of individuals in each category for each analysis is indicated above points (means  $\pm$  SEM) and bars. Y axes are scaled to reflect the typical range of observed values.

rate of approximately 50% (Sockman et al., 2023), ultimate drivers for age-related effects of any sort would seem unlikely. Our findings also imply that a single season of at least 30 days of 2 h/day of trapping effort (see Field Procedures in Methods) was sufficient to accurately assess the phenotype of an individual.

We also addressed whether phenotype was a by-product of either the location of our traps relative to the individual bird and the nest or of the timing of our trapping efforts relative to the individual's phenology. For both males and females, phenology of clutch initiation was nearly identical between the two phenotypes (Fig. 3). This similarity does not preclude phenotypic differences in the timing of foraging and other behaviours potentially associated with trap use. Also, we found no evidence for a difference between the trap and nontrap phenotypes in the male's proximity to traps; the distance from the nearest trap both to the males' singing perches and to their nests, even while controlling for their mate's phenotype, was not significantly different between phenotypes (Fig. 3). This is not surprising. With 50 trapping locations distributed across a roughly 15 ha site (Fig. 3), there were few locations with appropriate habitat that were very far from traps. Thus, it was surprising to find that the nests of nontrap females were significantly farther from the closest trap than the nests of trap females were. Although we cannot exclude that, for females, phenotype was a by-product of trap proximity and that positioning traps closer to their territories would have resulted in their capture, this seems unlikely. Any individuals of the trap phenotype that may have been misclassified as nontrap, either due to the location of the trap or to the possibility that they would have eventually entered a trap if given enough time, would not have explained why our nontrap set had higher measures of reproductive success (Fig. 5). Rather, such misclassifications would have added error to these analyses and thus reduced our ability to identify a difference between phenotypes in these and any other measures. It therefore seems more likely that distance to the nearest trap was due to another factor, for example, that it was a consequence of phenotype rather than a cause of how we assigned it. If nontrap females were avoiding traps due to neophobia or risk aversion, it is reasonable that they would have constructed their nests farther away from the feared, novel objects than females of the trap phenotype would (sensu Elvidge et al., 2016).

# Phenotype, Energetic Condition and Reproductive Success: Variation Due to Life-history Strategy?

We observed significant differences between phenotypes in our estimates of energetic condition (Fig. 4). These differences cannot be attributed to the seasonal timing of capture, which we controlled for in statistical models. And, for at least three reasons, the traps' seed bait was unlikely to have allowed individuals of the trap phenotype to increase their mass and therefore body condition, as well as their fat stores. First, measurements from the individual's first-ever capture were all that were used for these estimates. Second, we attempted to use only enough seed to lure the birds but not significantly supplement their nutrition. Third, and most importantly, a previous study on Lincoln's sparrows on our field site showed that stable isotopic values in plasma samples used to assess recent diet were not correlated with the frequency with which individuals visited seed-baited traps and that individuals' diets largely reflected natural prey present in their habitat (Beaulieu & Sockman, 2014). Thus, it seems unlikely that phenotypic differences in energetic condition were a result of trap use. Rather, they may have been its cause, as reasoned below.

Mass and energetic differences between phenotypes may have been associated with differences in how each phenotype resolves the life-history trade-off between current and future reproduction (Williams, 1966). One phenotype (reflected in our study as the trap phenotype) showed higher condition indices (Fig. 4) and lower reproductive success (in females; Fig. 5) possibly because it invests more in self-maintenance and thus in future reproduction as opposed to current reproduction. The other phenotype (reflected in our study as the nontrap phenotype) showed higher reproductive success (in females) and lower condition indices, possibly because it invests more in current reproduction at the cost of survival. This interpretation of our results would be consistent with previous hypotheses for the populationwide maintenance of two behavioural phenotypes (e.g. Cole & Quinn, 2014; Smith & Blumstein, 2008) were it not also the case that each phenotype was the opposite of what we had predicted for its particular life-history strategy. However, that prediction was based on our assumption that entering a trap is associated with risk-taking, neophilic or



**Figure 5.** Relationship between phenotype (N: nontrap; T: trap) and reproductive output in Lincoln's sparrows. The number of nests in each nest category is indicated at the top of each bar. Points (means  $\pm$  SEM) are provided only for visual comparison; statistical analyses were based on the ordinal values indicated by the bar shading. *P* values refer to the effect of each sex's phenotype on each measure of reproductive output.

exploratory behaviour. Support for this assumption awaits several additional assessments, including determining whether the two phenotypes show a similar difference in approach towards other novel objects but no such difference in approach towards familiar objects. In the absence of such support, our assumption may be false, and it is even plausible that the opposite is true, at least for exploratory behaviour. We intentionally positioned traps, in part, based on where we thought Lincoln's sparrows would be most likely to forage, but that decision may have attracted less exploratory, more risk-averse individuals.

Several studies have reported relationships between behavioural phenotype and fitness components, as mentioned in the Introduction (Dingemanse & Réale, 2005). In Gouldian finches, Erythrura gouldiae, red-headed individuals are less exploratory (but also more aggressive) than their black-headed counterparts (Mettke-Hofmann, 2012; Williams et al., 2012), and red-headed males become more aggressive under competitive social conditions (Pryke & Griffith, 2009). Because male Gouldian finches provision chicks more than females (Fragueira et al., 2021), this elevated aggressiveness strongly decreases the reproductive performance of red-headed pairs in competitive environments. In contrast, under more relaxed social conditions, their reproductive performance remains similar or can even be higher than that of black-headed males (Brazill-Boast et al., 2013; Pryke & Griffith, 2009), suggesting in that case that the higher exploratory tendency of black-headed males is more costly than the aggressive tendency of red-headed males. If this pattern applies to Lincoln's sparrows, lower breeding success of more exploratory (and possibly less aggressive) individuals would suggest that the birds of our study were breeding in a low competitive environment. However, at this point, we have no evidence for an association between trap phenotype and either exploratory or aggressive behaviour. Moreover, we found that, in contrast to Gouldian finches, the reproductive performance of Lincoln's sparrows depended on the phenotype of females (and not males), which are not involved as much as males in aggressive interactions (Speirs & Speirs, 1968). The lower reproductive performance of females of the trap phenotype is therefore unlikely related to the conflicting expression of aggressiveness and parental care but rather to the conflicting expression of exploration and parental care. For instance, during the nestling rearing period, females of the trap phenotype may spend more time than nontrap females feeding for themselves than provisioning their nestlings, which could explain why their body condition was higher while their reproductive performance was lower (assuming males do not increase their provisioning rate in response to the decreased provisioning rate of females).

The relationship between behavioural phenotype and fitness components apply to a diversity of systems. For example, a population of great tits, *Parus major*, showed individually consistent differences in the speed of exploratory behaviour (Dingemanse et al., 2002), a behaviour shown by another study on this species (Drent et al., 2003) to have considerable heritability. Females that are slower in this behaviour show elevated reproductive success, whereas the opposite relationship applies to males when reproductive success is measured as fledgling mass (Both et al., 2005). Phenotype in this population is also associated with survival but varies between years, each year favouring the sexes in opposing directions (Dingemanse et al., 2004). Interestingly, but not surprisingly, this tends to favour disassortative pairing, regardless of year (Both et al., 2005).

In orb-weaving spiders (*Larinioides sclopetarius*), sons of aggressive parents sire more offspring than sons of nonaggressive parents, a phenomenon that apparently promotes assortative mating (Kralj-Fišer et al., 2013). In bighorn rams, *Ovis canadensis*, docile and bold rams show higher survival and higher reproductive success than nondocile and shy rams (Réale et al., 2009). And bold behaviour in male fiddler crabs is associated with more time spent courting females and thus elevated mating success (Reaney & Backwell, 2007). In short, several studies support the relationship

between behavioural phenotype and reproductive success, some in ways consistent with at least some of our findings and others not.

# Implications of Assortative Mating

Among assortative pairings only, the proportion that was of the trap phenotype (68%) was close to the predicted 69% based on random pairing, equal distribution of the sexes between the two phenotypes and the frequency of each phenotype. However, assortative pairing as a whole occurred much more frequently (67%) than would be expected under random pairing with no plasticity in phenotype (52%), given the parameters above. Therefore, either pairing must not have been random or phenotype must flexibly change to match that of the mate (e.g. Holtmann & Dingemanse, 2022).

There are several possible mechanisms that could have sorted the phenotypes spatially and thus elevated the probability of their pairing, for example through phenotypic differences in competition for localized resources (e.g. Pryke & Griffith, 2009) or through aversion or attraction to locations of the traps or other objects or locations. However, although phenotype affected female location (at least their nests), we do not have strong evidence that it affected male location. Thus, we do not currently have evidence that differential spatial distributions played a major role in bringing similar phenotypes together, although that idea remains a possibility. Furthermore, we do not have evidence that any additional traits are correlated with phenotype and thus could serve as a basis for mate choice. Notwithstanding this, the implications of the bias are perhaps more interesting anyway, particularly in light of the fact that whether or not pairing was assortative did not seem to affect reproductive success (Fig. 5); only the female's phenotype did.

Phenotypic correlation between mated individuals, whether by assortative pairing or plasticity, can have important evolutionary and conservation implications (Martin & Jaeggi, 2021). Assortment can produce an association between the values of an individual's genetic traits and their mate's fitness (Hamilton, 1964a, 1964b). If assortment is strong enough for long enough, reproductive isolation can follow even if the phenotypic variation on which the sorting is based is nongenetic (e.g. Najarro et al., 2015). When mating is random, traits that converge on a common value between mates due to plasticity can be determined not only by direct but also by indirect genetic effects, due to heritable variation in a mate's phenotype, leading to evolution in the behaviour itself (Bijma & Wade, 2008). At this point, we do not know whether variation in trap phenotype is heritable. Nevertheless, these possible scenarios raise questions regarding how various field methodologies (e.g. use of traps) could catalyse or even drive mating patterns, the evolution of behavioural traits and reproductive isolation. Moreover, our findings may extend beyond the role of traps in field ornithology and to the myriad novel objects widely distributed in animal ecosystems, from novel predators and food resources to those found in the increasingly human-developed world, from roads and buildings to other structures, such as cell phone towers. Perhaps the presence of such natural and human-made novelties could contribute to animal mating patterns broadly.

Thus far, we cannot extend the phenotype we discovered to a more general one, such as one related to neophobia, risk aversion or exploratory behaviour. Still, our findings strongly suggest that the phenotypes we observed are part of a more general phenotypic difference associated with fitness components. It would be difficult otherwise to reconcile a specific avoidance of traps with some of our observations, in particular, the phenotypic associations with multiple fitness components. Our findings are relevant to other studies using traps on wild animals, but the implications extend well beyond that to the possible roles of novel objects and situations affecting not just fitness but also population dynamics, as well.

In summary, we describe a phenotype based on trappability that predicts measures of both energetic condition and current reproductive success consistent with life-history theory and the presence of individual variation in condition. Surprisingly, what we assumed would be the more exploratory, risk-taking phenotype turned out to be the phenotype with higher condition, exactly the opposite of that predicted by the above theory. Future work should aim to determine whether trappability is indeed indicative of risktaking, exploratory behaviour or just the opposite, where foraging in trap locations is risk averse.

### **Author Contributions**

**Keith W. Sockman:** Conceptualization, Methodology, Formal Analysis, Investigation, Resources, Data Curation, Writing – Original Draft, Writing – Review and Editing, Visualization, Supervision, Project Administration, Funding Acquisition. **Michaël Beaulieu:** Investigation, Writing – Review and Editing.

#### **Data Availability**

The data set for this study is provided as supplementary material.

### **Declaration of Interest**

None.

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#### **Supplementary Material**

Supplementary material associated with this article is available, in the online version at https://doi.org/10.1016/j.anbehav.2023.01. 015.

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