

i or β_σ), and between evolvability ($I_A:V_A$ divided by squared phenotypic trait mean) and mean-standardized selection gradients (β_μ). Using 24 years of data from an island population of Savannah sparrows, we show that, across diverse traits, h^2 declines with the strength of selection, whereas I_A and I_R (V_R divided by squared trait mean) are independent of the strength of selection. Within trait types (morphological, reproductive, life-history), h^2 , I_A , and I_R are all independent of the strength of selection. This indicates that certain traits have low heritability because of increased residual variance due to the age at which they are expressed or the multiple factors influencing their expression, rather than their association with fitness.

KEY WORDS: Animal model, fitness, Fisher's fundamental theorem, mean-standardized selection gradient, natural selection, selection intensity, Savannah sparrow.

A major challenge in evolutionary biology is explaining variation in the evolutionary potential among traits (Houle 1992; Merilä and Sheldon 1999). Historically, narrow-sense heritability (h^2) has been used as a measure of evolutionary potential; h^2 estimates the relative importance of additive genetic variance (V_A) in shaping phenotypic variance (V_P) ($h^2 = V_A/V_P$) (Falconer and Mackay 1996). A common observation is that the phenotypic traits that have the largest influence on an individual's fitness have the lowest h^2 (Mousseau and Roff 1987; Falconer and Mackay 1996; Merilä and Sheldon 1999). The traditional explanation is that directional selection on traits important for fitness ("fitness traits") eliminates inferior alleles and fixes superior alleles, thereby limiting evolutionary potential by exhausting genetic variation in phenotypic traits in direct proportion to their effect on fitness, in accordance with Fisher's fundamental theorem (Fisher 1930; Kimura

1958; Gustafsson 1986; Falconer and Mackay 1996; Teplitsky et al. 2009). However, heritability is problematic for comparing levels of additive genetic variation of different traits. Because $h^2 = V_A/V_P$, and because V_P comprises both heritable (V_A) and nonheritable (environmental and nonadditive genetic) residual variation ($V_R = V_P - V_A$), the relatively low heritability of fitness traits could be the result of elevated V_R rather than exhausted V_A (Price and Schluter 1991; Houle 1992; Merilä and Sheldon 1999; Hansen et al. 2011).

According to the univariate breeders' equation, the evolutionary response to selection (R) equals h^2 times the selection differential (S , the covariance between a trait and relative fitness; $R = h^2S$) (Lynch and Walsh 1998; Hansen et al. 2011). Because h^2 measures the relative amount of additive genetic variation underlying a particular trait at a particular time, it only allows for

a comparison of the evolutionary response of traits under equally strong selection (Postma 2014). However, by definition fitness traits are under stronger selection than nonfitness traits (Mousseau and Roff 1987; Falconer and Mackay 1996; Merilä and Sheldon 1999). Thus, h^2 by itself cannot be used to compare the evolutionary potential of different traits.

Houle (1992) introduced the concept “evolvability,” which is the “expected percent change in a trait under a unit strength of selection” (Hansen et al. 2011). Evolvability is best measured as the mean-standardized additive genetic variance underlying a trait (Garcia-Gonzalez et al. 2012). The coefficient of additive genetic variation ($CV_A = \text{square root of } V_A \text{ divided by the phenotypic mean of the trait, multiplied by 100}$) is frequently used to measure evolutionary potential (Teplitsky et al. 2009; Garcia-Gonzalez et al. 2012). However, I_A , which is V_A divided by the squared phenotypic trait mean, multiplied by 100 (Houle 1992), has a more direct evolutionary interpretation and is preferable for comparing estimates of evolutionary responses of different traits under directional selection (Hansen et al. 2011).

Fitness traits such as longevity are themselves affected by numerous physiological, morphological, and behavioral traits, each of which in turn is affected by environmental factors. As a consequence, fitness traits could be expected to have relatively high V_R because of the many possible sources of environmental variation that influence traits that are “one step further down the causal pathway from genes to phenotype” (Price and Schluter 1991). The same would be true for traits that integrate environmental influences across the entire lifespan as opposed to being expressed only at a specific age. According to this reasoning, fitness traits would be predicted to have lower h^2 than traits under weaker selection, not because of low V_A but because of high V_R (Merilä and Sheldon 1999).

On the other hand, because fitness traits are likely to have more loci affecting their expression, they present a bigger mutational target than simple (nonfitness) traits, which potentially results in faster replenishment of V_A , as originally speculated by Kimura (1958). This leads to the opposite prediction, that V_A should be *greater* in traits closely linked to fitness (Houle et al. 1996; Houle 1998; Merilä and Sheldon 1999). Despite substantial theoretical and empirical work, this issue remains unresolved (Merilä and Sheldon 1999; Teplitsky et al. 2009).

The few studies that have quantified additive genetic variance and residual variance in natural vertebrate populations have produced conflicting results. In red-billed gulls (*Larus novaehollandiae*), h^2 and CV_A declined as the trait’s correlation with fitness increased (Teplitsky et al. 2009). In contrast, in two populations of nest-box-breeding birds and two populations of ungulates, only h^2 was negatively correlated with fitness, whereas CV_A showed no correlation or was positively correlated with fitness (Kruuk et al. 2000; Merilä and Sheldon 2000; McCleery et al. 2004; Coltman et al. 2005).

Although groundbreaking, these field studies were limited by the small number of phenotypic traits examined, and they were often confounded by a history of human management of the study populations (e.g., provisioning of artificial nest sites for birds, culling of ungulate herds) that may have altered selection and reduced environmental and/or genetic variance (Houle 1992; Coltman et al. 2005). Moreover, studies so far have examined the relationship between a trait’s correlation with fitness and h^2 or CV_A across relatively few fundamentally different types of traits (Mc-

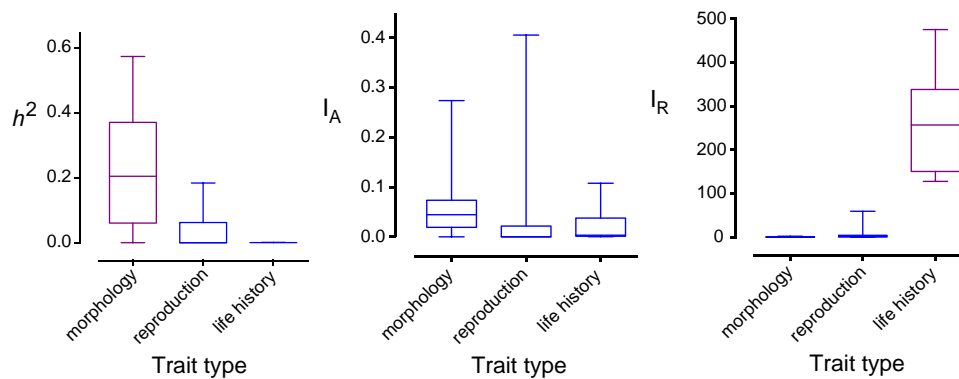


Figure 1. Box and whiskers plots showing heritability (h^2), evolvability (I_A), and mean-standardized residual variance (I_R) for three trait types ($N = 50$ morphological traits, 26 reproductive traits, 12 life history traits) in Savannah sparrows on Kent Island, New Brunswick, Canada. Horizontal line indicates median, box indicates 10th and 90th percentiles, and whiskers indicate minimum and maximum values. I_A and I_R are given (

Table 1. Heritability (h^2), SE of h^2 , I_A ($= V_A$ divided by the squared phenotypic mean, multiplied by 100), SE of V_A , I_R ($= V_R$ divided by the squared phenotypic mean, multiplied by 100), selection intensity ($i = \beta_\sigma$)

Table 1. Continued.

A. Females								
Trait type	Trait	h^2	SE h^2	I_A	SE V_A	I_R	i	β_μ
Morphology	Mass	0.140	0.143	0.1072	0.382	0.6571	-0.01	-0.17
Morphology	Wing length	0.505	0.189	0.0274	0.477	0.0269	0.02	1.11
Morphology	Tarsus length	0.518	0.224	0.0422	0.083	0.0393	0.08	2.82
Morphology	Bill length	0.232	0.299	0.0481	4.006	0.1588	0.12	2.62
Morphology	Bill depth	0.177	0.341	0.0240	1.246	0.1116	0.05	1.54
Reproduction	Clutch size	0.056	0.139	0.1627	0.070	2.7689	-0.03	-0.31
Reproduction	No. hatched	0	0.096	0.0015	0.326	37.0394	0.12	0.23
Reproduction	No. fledged	0	0.103	0.0000	0.348	54.6284	0.17	0.24
Reproduction	× offspring mass	0	0.186	0.0000	3.883	2.5163	0.12	1.16
Reproduction	× offspring wing	0.101	0.198	0.2517	1.021	2.2353	0.09	0.73
Reproduction	× offspring tarsus length	0	0.262	0.0000	0.510	0.4951	0.14	2.11
Reproduction	Max offspring mass**	0	0.170	0.0000	3.200	1.9285	0.14	1.73
Reproduction	Max offspring wing**	0.184	0.239	0.2645	0.861	1.1768	0.07	0.64
Reproduction	Max offspring tarsus** length	0.051	0.306	0.0221	0.562	0.4088	0.1	1.61
Reproduction	Laying date	0.135	0.167	0.0218	7.120	0.1398	-0.08	-2.67
Reproduction	Interclutch interval*	0	0.438	0.0001	16.150	3.4868	-0.18	-1.07
Reproduction	Replacement interval*	0		0.0001	5.629	22.1690	0.07	0.15
Reproduction	Postfledging parental care*	0	0.599	0.0000	21.199	6.9464	0.15	0.69
Reproduction	EPP*	0	0.286	0.0000	487.860	0.0000	0.22	0.22
Reproduction	Brood sex ratio*	0	0.199	0.0000	0.0169	0.0000	0.06	0.07
(v) Life history								
Life history	Lifetime mates	0.001	0.040	0.1079	0.027	140.1903	1.65	1.09
Life history	Lifetime nests**	0	0.045	0.0066	0.171	272.2203	1.79	1.06

Table 1. Continued.

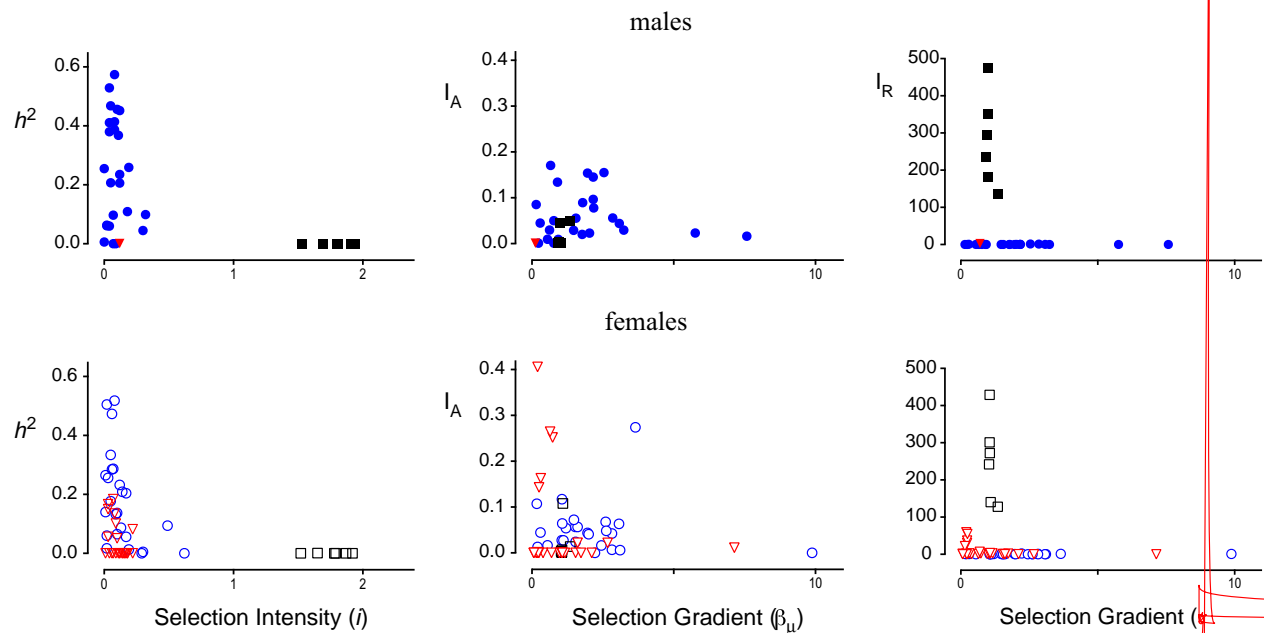
A. Females								
Trait type	Trait	h^2	SE h^2	I_A	SE V_A	I_R	i	β_μ
(ii) Juveniles								
Morphology	Condition (mass/wing)**	0.456	0.195	0.1538	0	0.1820	0.10	1.96
Morphology	Condition (mass/tarsus)**	0.109	0.269	0.0440	0	0.3582	0.18	3.08
Morphology	Mass	0.529	0.198	0.1707	0.236	0.1520	0.04	0.66
Morphology	Wing length	0.574	0.113	0.0290	0.312	0.0215	0.08	1.47
Morphology	Tarsus	0.411	0.206	0.0501	0.115	0.0720	-0.04	-0.77
Morphology	Tail length	0	0.402	0.0040	5.424	0.4700	0.07	2.03
(iii) 1-year-old								
Morphology	Condition (mass/wing)**	0.207	0.118	0.0686	0	0.2550	-0.05	-0.93

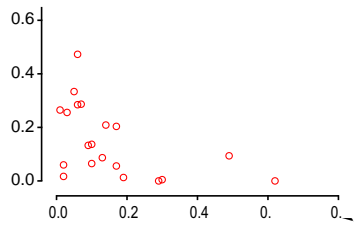
Table 2. Slopes of linear regressions (\pm SE) of heritability (h^2) on selection intensity (i , absolute value), and of I_A ("evolvability," which is V_A divided by the squared phenotypic mean, multiplied by 100) and the mean-standardized coefficient of residual variance (I_R) on the mean-standardized selection gradient (β_μ , absolute value) for phenotypic traits ($N = 88$, counting features measured at different ages or in different sexes as separate traits) measured on Savannah sparrows on Kent Island, New Brunswick, Canada. Results are broken down by general trait type and sex. Results were similar after removal of highly correlated traits ($N = 60$).

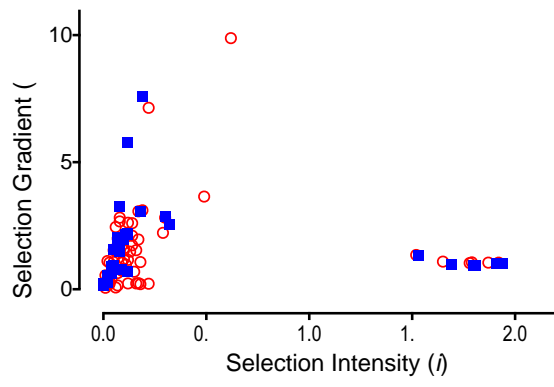
Trait type	Sex	Number of traits	h^2	I_A	I_R
Morphology	Male	25	$-0.36 (\pm 0.47)$	$-0.003 (\pm 0.006)$	$-0.04 (\pm 0.06)$
Morphology	Female	25	$-0.50 (\pm 0.19)$	$-0.00 (\pm 0.01)$	$0.05 (\pm 0.06)$
Reproduction	Female	25	$-0.40 (\pm 0.20)$	$-0.01 (\pm 0.02)$	$-3.37 (\pm 2.38)$
Life history	Male ¹	6	---	$0.104 (\pm 0.058)$	$-367.5 (\pm 361.7)$
Life history	Female	6	$0.002 (\pm 0.001)$	$0.015 (\pm 0.173)$	$-559.0 (\pm 363.1)$
All traits combined	Male ²	32	$-0.14 (\pm 0.05)$	$-0.00 (\pm 0.01)$	$-0.08 (\pm 0.08)$
All traits combined	Female	56	$-0.08 (\pm 0.03)$	$-0.00 (\pm 0.01)$	$-0.03 (\pm 0.04)$

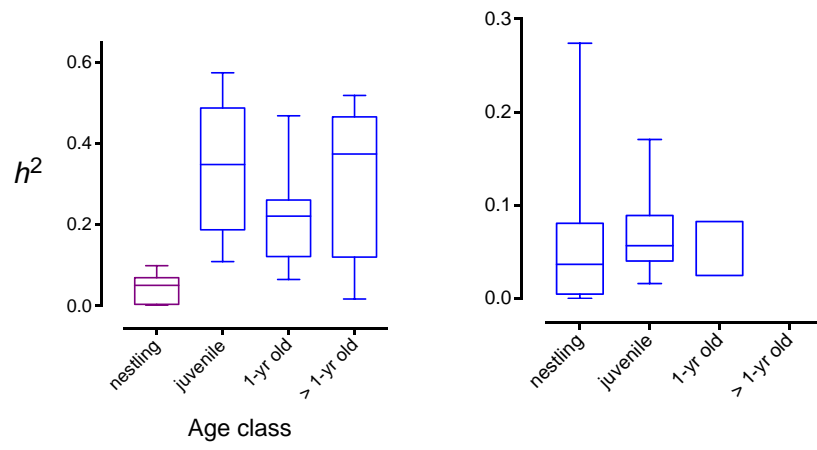
¹Slope not calculated because $h^2 = 0$ for all male life history traits.

²Includes postfledging parental care by males.









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DATA ARCHIVING

The doi for our data is 10.5061/dryad.dv0qt.2.

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