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"HIDDEN" REPRODUCTIVE CONFLICT BETWEEN MATES IN A WILD BIRD POPULATION

Jon E. Brommer[1,2] **and Kalev Rattiste**[3,4]
[1]*Bird Ecology Unit, Department of Biological and Environmental Sciences, P.O. Box 65 (Viikinkaari 1), FIN–00014 University of Helsinki, Helsinki, Finland*
[2]*E-mail: jon.brommer@helsinki.fi*
[3]*Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Riia 181, EE 51014, Tartu, Estonia*
[4]*E-mail: Kalev.Rattiste@emu.ee*

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Environmental conditions experienced by a female prior to reproducing may be influenced by her mate. Part of such an indirect effect of a male on his partner's reproduction may be genetic (indirect genetic effect). However, a female's direct and a male's indirect genetic effects need not align. We analyzed 10,652 records of seasonal timing of laying, an important reproductive trait in many organisms, of 1864 male and 1916 female common gulls *Larus canus* collected during 37 years. We show that there is both a direct (female) and an indirect (male) genetic effect (explaining 14.5% and 4.8% of the REML estimated variance in laying date, respectively), but these are significantly negatively correlated (−0.53 ± 0.22 SE), indicating that genes for early laying in females are associated with genes for a delaying male effect on his partner's laying date (and vice versa). There is strong selection for laying early in this population, and these sexually antagonistic genetic effects may contribute in maintaining the variation in laying date. Our findings provide an empirical demonstration of a hitherto largely unstudied level of conflict between mates, with important ramifications for our understanding of evolutionary dynamics and mate choice in nature.

KEY WORDS: **Animal model, heritability, long-term data, natural selection, quantitative genetics, sexual conflict, sexual selection.**

Quantitative genetics describes the response to selection on a trait (or complex of traits) (Fisher 1958; Falconer and MacKay 1996). In the coarsest sense, variation in a trait is composed of genetic and environmental effects, where only the former contributes to a response to selection. Nevertheless, a major part of an individual's environment is often determined by its conspecifics, creating an indirect effect of one individual (or group of individuals) on the phenotype of a focal individual (Rossiter 1996), and part of such indirect effects may be heritable (indirect genetic effect, Moore et al. 1997; Moore and Pizzari 2005). Most empirical work on indirect genetic effects concern parent–offspring relationships, where the natal environment in which offspring develop is created by the (related) parent and this environment has a genetic component (Mousseau and Fox 1998; Wilson and Reale 2006). Indirect genetic effects between unrelated individuals are rarely studied under laboratory conditions (but see Wolf 2003; Mutic and Wolf 2007) and are, to our knowledge, unexplored in wild populations. The standard quantitative genetic approach largely ignores indirect effects between unrelated individuals, or considers them as environmental effects only. However, if such indirect effects are heritable and under selection, they will evolve, and may either speed up or slow down evolution of a trait depending on whether they are selected in the same or opposite direction as the direct genetic effects (Moore et al. 1997; Wolf et al. 1998; Wolf 2003). One potentially common indirect effect between unrelated individuals may occur if a male can improve his partner's prereproductive condition, for example by feeding her. Such indirect effects are likely to be of paramount importance for the pair's fitness. Part of a male's indirect effect on his partner's reproduction may be heritable, but, to our knowledge, no study to date has documented male indirect genetic effects on his partner's reproduction.

The seasonal timing of reproduction (laying date) is a crucial fitness-related trait in many organisms including birds (Rowe et al. 1994), and this reproductive trait is expressed by the egg-laying female. In our study species, the common gull *Larus canus*, clutch size is invariant (three eggs), and laying date is thus presumably a key reproductive trait in this species. We view a male's potential indirect effect on laying date as a nonreciprocal social interaction (Moore et al. 1997), because a male may influence a female's prelaying environment (and thereby her laying date), but a female's trait expression (laying the season's first egg) cannot influence events prior to it. A male may affect his partner's prelaying environment by an (unknown) trait; for example his ability to arrive early to the colony and quickly establish and defend a breeding site, his ability for courtship feeding, and his timing of spermatogenesis and copulation prowess. As a result of this interaction, a female's laying date is affected by the direct (female) genetic effect and an environmental component consisting of environmental effects associated with the female, plus the effect the male has on his partner's prelaying environment. The latter indirect effect may itself consist of a genetic and a nongenetic component (Moore et al. 1997). Here, we introduce a REML mixed model procedure to describe the direct (female) and the indirect (male) effects on laying date, a female linked trait. To explore the genetics of this indirect effect, we use information from the population's pedigree within the mixed modeling procedure (animal model, Lynch and Walsh 1998). The animal model approach allows to calculate both the indirect genetic effect and its correlation with the direct genetic effect. Hence, evolutionary insights into social interactions between mates can be achieved on the genetic level, also in absence of knowledge of how males would phenotypically exert an indirect effect on their partner.

We here analyze 37 years of data on laying dates recorded in an individual-based study of common gulls breeding in Estonia. The common gull's longevity in combination with a pair retention rate of 67% (Rattiste and Lilleleht 1986) allows us to estimate the effects each of the mates has on laying date. By using information on relatedness, derived from the population's pedigree, we further study the genetic architecture of and selection on this important form of social interaction.

Methods

STUDY POPULATION AND METHODS

Data on common gulls were collected in 1968–1983 and 1986–2006 on three offshore islets of the Matsalu National Park, Estonia (detailed in Rattiste 2004). Laying date (date when a pair laid the season's first egg) was based on daily checks of the colonies. At their first breeding event, adult birds were sexed and individually marked with a metal ring (in case they were not ringed as a nestling) and a plastic ring with a clearly visible individual code. Adults were identified in later years by direct observations from a hide without catching them. Laying date of the first egg was known in 11,624 clutches of 2210 males and 2262 females. An individual had on average about two partners during its recorded breeding life span (females 2.02 ± 0.03 [range: 1–12], males 2.08 ± 0.03 [range: 1–10]). There were 346 pairs in which neither the male nor the female bred with another partner, forming 8.4% (972/11,624) of all observations. We omitted these "faithful" pairs from the analyses to reliably separate male and female effects on laying date (thus using 10,652 laying dates of 1864 males and 1916 females for the analyses).

STATISTICAL MODELS

We assumed that the *i*th laying date could be described by the models

$$d_i = \mu_F + year + female + male + \varepsilon_i, \tag{1a}$$

$$= \mu_F + year + (a_f + pe_f) + (a_m + pe_m) + \varepsilon_i, \tag{1b}$$

where μ_F is the overall fixed effect mean encompassing a number of fixed effects (see below). In the phenotypic model (1a), random effect *year* estimates variance across years and random effects *female*, and *male* specify deviations from the overall fixed-effect mean due to variation across females and males, respectively, with ε_i specifying the residual error. Using an animal-model approach (Lynch and Walsh 1998), the sex-specific phenotypic effects can be broken down (eq. 1b) into random effects for a female's (direct) and a male's (indirect) genetic effects (a_f and a_m, respectively), and effects for the permanent environmental effects (pe_f and pe_m for female and male, respectively). The permanent environment effect includes among-individual sources of variance that are conserved across records but are not due to additive effects (e.g., individual-specific environmental, maternal environment, any nonadditive genetic effects, see Lynch and Walsh (1998) and Kruuk (2004) for further details). We explicitly consider in some detail maternal and common temporal environmental effects (see below). The partitioning of phenotypic male effect into its additive genetic and permanent environmental components can be achieved because the degree of resemblance in laying dates across the partners of a male's male relatives will be due to male additive genetic effects, because these male relatives do not share the same environment as the focal male. Equation (1) was solved using Restricted Maximum Likelihood (REML) implemented in ASReml (VSN International), which estimated the variance for each random effect term. In addition, the genetic covariance between direct (female) and indirect (male) genetic effects was estimated on the basis of resemblance across related individuals of the opposite sex. Note that of all the terms in equation (1), only the genetic covariance $\mathrm{cov}(a_f, a_m)$ can be estimated in an additive, single-trait model.

To test the statistical significance of the terms in the full model (eq. 1b), we increased model complexity in steps. Statistical significance of entering each random effect was tested using a likelihood-ratio test (LRT), calculated as $-2 \times$ the difference in log likelihood between models with and without a particular random effect. This likelihood ratio was tested as a chi-square distribution in which the number of variance components added were the associated degrees of freedom (always one in our case). We started from a model with fixed effects and residuals only (model 1). We then tested for the effect of year (model 2), followed by the phenotypic effects of female (model 3) and male (model 4). Thereafter we tested for the significance of partitioning these effects into genetic and nongenetic components for females (model 5) and males (model 6). Lastly, the genetic covariance between direct (female) and indirect (male) effects was included (model 7), and tested for by an LRT between model 7 and model 6.

Additive genetic (co)variance was estimated using the population's pedigree, which was based on all recruits recorded up to and including 2006, and consisted of 1130 recruits with both parents known, eight with only their father and four with only their mother known. In total, relatedness was known between 46% (1731/3780) of individuals considered here. Due to sex biased dispersal in this species, 80% of the recruited offspring were males, and there were 1017 male individuals linked to at least one other male in the pedigree versus 391 females linked to at least one other female. Across sexes, 623 females had at least one male relative and 818 males had at least one female relative in the pedigree. Genetic parentage of recruits was inferred on the basis of the social status of the parents, which is correct for females. Paternal links may contain some errors, because DNA fingerprinting revealed that 3.6% of common gull chicks resulted from extra-pair copulations in a Polish population (Bukacińska et al. 1998). However, such low rates of extra-pair paternities are unlikely to bias estimates of additive genetic (co)variance components (Charmantier and Réale 2005).

We included three fixed factorial effects. First, we coded for which of the three islets the breeding occurred (colony effect). Second, we included the status of a breeding pair, describing that they were either a newly established pair or the same pair as in the previous season, or unknown. Lastly, we included the breeding experience of male and female parents. Breeding experience was a count of the number of years an individual has been part of the breeding population with first breeding counted as one (see also Rattiste 2004). On average, males start to breed at 3.2 years, and females at 3.7 years, but because the exact age could not be determined for many individuals, we used breeding experience as a proxy for age.

The proportion of phenotypic variance explained by direct additive genetic effects (heritability h^2) and indirect additive genetic effects was calculated by using the sum of all REML estimates of variances as the phenotypic variance. Comparison of heritability based on REML variance components across different studies is not meaningful when these studies differ in their fixed effect structure (Wilson 2008). In particular, we accounted for annual variation as a random effect such that variation across years is included in the REML estimate of phenotypic variance. Many other studies correct for annual variation in mean laying date by including year as a fixed effect, which is likely to drastically reduce the REML estimate of phenotypic variance and produces, all else being equal, a higher heritability than a model in which yearly variation is viewed as a random effect. To aid in comparison across studies, we therefore also provide the observed phenotypic variance in laying date, prior to conditioning on the fixed effects (see Wilson 2008 for a discussion).

SELECTION

Selection was formally quantified following Lande and Arnold (1983). The annual linear standardized selection gradients β' on phenotypic laying date were calculated for recruitment and female survival as the linear term in a least-squares linear regression of phenotypic laying date standardized to zero annual mean and unit annual standard deviation on relative recruitment or survival. Annual nonlinear standardized selection gradients γ' were calculated as twice the coefficient of standardized laying date squared in a linear regression model on relative recruitment or survival that also included the linear term. Relative recruitment was the observed number of recruits (offspring that bred later in life) of both sexes produced in a breeding in a given year divided by that year's average recruitment (total number of recruits of both sexes, divided by the number of breeding pairs). Relative survival was calculated as an individual's observed survival in a given year (died [0] or survived [1]) divided by that year's adult survival probability (fraction of same-sex individuals that survived). All linear regression model describing the selection included a constant.

On average, 94% (SD = 4.8%, range: 74%–99%) of nest owners (both males and females) were identified. This value is conservative because unidentified nest owners may have actually been identified later in the season in case they renested after the initial clutch failed. Nest owners that could not be individually identified before clutch failure mainly were new individuals that did not have a plastic ring and therefore needed to be trapped. Given that there is selection for earlier laying (see main text), selection estimates are conservative with respect to

Table 1. Hierarchical mixed models of 10,652 laying dates of 1916 common gull females and 1864 males forming 4157 pairs recorded over 37 years.

Model	Terms								Test	
	$V(year)$	$V(female)$	$V(male)$	$V(a_f)$	$V(pe_f)$	$V(a_m)$	$V(pe_m)$	residual	LogL	χ^2
1	–	–	–	–	–	–	–	29.7 (0.27)	−23403.4	
2	10.5 (2.5)	–	–	–	–	–	–	19.4 (0.27)	−21239.8	4327.2C
3	10.5 (2.5)	6.6 (0.33)	–	–	–	–	–	13.5 (0.20)	−20416.7	1646.2[1]
4	10.6 (2.5)	5.8 (0.33)	3.1 (0.25)	–	–	–	–	11.8 (0.19)	−20254.2	325.0[1]
5	10.6 (2.5)	–	3.1 (0.25)	4.1 (1.2)	1.7 (1.2)	–	–	11.8 (0.19)	−20249.2	10.0[2]
6	10.6 (2.5)	–	–	4.1 (1.2)	1.7 (1.2)	1.3 (0.51)	1.8 (0.53)	11.8 (0.19)	−20245.9	6.6[3]
7	10.58 (2.5)	–	–	4.52 (1.2)	1.29 (1.2)	1.49 (0.53)	1.55 (0.53)	11.84 (0.19)	−20243.7	4.4 [3]
					$\mathrm{cov}_A = -1.38 \pm 0.59$					
p	0.338 (0.053)			0.145 (0.040)	0.041 (0.038)	0.048 (0.017)	0.050 (0.017)	0.379 (0.031)		
r					$r_A = -0.53 \pm 0.22$					

The estimated variance with standard error in brackets is given for terms that were included in the model, with "–" indicating terms that were not included. Random effect terms are sequentially entered and tested, where the significance of each term is based on the increase in log-likelihood (LogL), starting with the model with fixed effects and residuals only (model 1). Terms are the variance (*V*) for year (*V*(*year*)), the sex-specific phenotypic variance for females (*V*(*female*)) and males (*V*(*male*)). The latter two were split into their components, the additive genetic variance ($V(a_f)$ and $V(a_m)$) and permanent-environmental variance ($V(pe_f)$ and $V(pe_m)$), of females (*f*) and males (*m*), respectively. In model 7, in addition to all terms, the genetic covariance between direct (female) and indirect (male) genetic effects ($\mathrm{cov}[a_f, a_m]$), is included. We report the likelihood-ratio test (χ^2 statistic with associated df of one) between the given model and the model that is one hierarchical step higher (i.e., 2 vs. 1, 3 vs. 2, etc). Significance of LRT:

[1] $P < 0.001$; [2] $P < 0.01$; [3] $P < 0.05$. For the final model (model 7), the proportion *p* of variance due to the different causal factors calculated over the sum of all REML estimates of variance are presented with their standard error. The fixed effect structure is the same in all models and is presented in Table 2. Phenotypic variance in laying date prior to conditioning on the fixed effects was 38.7. The proportion of variance due to female additive genetic effects $V(a_f)$ is the heritability (h^2).

unidentified adults, because unidentified individuals were individuals that tended to breed late in the season and whose clutch failed or was destroyed before the individual could be caught.

We considered annual selection up to and including the year 2002 (total of 33 years) in order for recruits to be recorded by the age of four years when most of them started their breeding career, and to have as accurate survival estimates for adults as possible. Temporal consistency in annual selection was tested by a sign test. Statistical significance of annual selection was tested using a generalized linear model (GLM) on the observed recruitment (0, 1, 2, or 3 offspring) and survival (survived, 1; died, 0) with either a log link and Poisson errors or a logit link and binomial errors for recruitment and survival selection, respectively. Because a GLM deals with (log or logit) transformed data, significance may or may not reflect the effects size of the standardized selection gradients β' and, in particular, γ'. We focused on phenotypic selection and did not analyze selection on the predicted breeding value (PBV) for direct (female) and indirect (male) genetic effects because calculating selection on PBV is performing a statistical analysis on model-derived statistics, which has been shown to be biased (Hadfield 2008).

Results

We stepwise constructed the most parsimonious mixed model on repeated observations of laying date recorded for 3780 individuals, where at least one of the mates of each pair bred with another partner during its breeding career (Table 1). There were strong annual effects on laying date (model 2). Both females (model 3) and males (model 4) had highly significant phenotypic effects on laying date. Using pedigree information from this population, we partitioned the sex-specific phenotypic effects on laying date further into their genetic versus individual-specific environmental components using an animal model approach. We found significant female (i.e., direct) genetic effects a_f (model 5) and male (i.e., indirect) genetic effects a_m (model 6). Lastly, we included the genetic covariance between direct (female) and indirect (male) genetic effects ($\mathrm{cov}[a_f, a_m]$) and found this to be significantly negative (model 7). Hence, on the same genome, loci that in males advance his partner's laying date, delay laying when expressed in females (and vice versa).

The fixed effects part of the final model (Table 2) showed that laying date differed across colonies. Furthermore, changing a partner led to a delay in laying date of 1.8 days relative to a previously established pair. Lastly, the breeding experience (a proxy of age) of males and females affected laying date.

Table 2. **Fixed effects of mixed-model 7 in Table 1 (the same fixed-effect structure was used in the other models).**

Fixed effect	coefficient	*F*-test	*P*
Constant	43.0±0.55	$F_{1,10588}$=4890.7	<0.001
Status		$F_{2,10588}$=186.6	<0.001
New partner	1.84±0.096		
Unknown	5.67±2.5		
Colony		$F_{2,10588}$=6.6	0.01
Female experience		$F_{26,10588}$=30.1	<0.001
Male experience		$F_{27,10588}$=23.7	<0.001

Categorical fixed effects were: the breeding status of a pair (new pair or prior-established pair (or considered unknown in three cases)), breeding colony, and breeding experience (the number of years individual was part of the breeding population). Effect of "Status" is given relative to a prior-established pair. *F*-tests are conditional Wald's tests.

Annual variation accounted for 34% of the variation in laying date. Differences across females were mostly due to direct (additive) genetic effects rather than nongenetic individual-specific effects, with a heritability (h^2) of 14.5%. Males had a small, but significant, indirect additive genetic effect explaining 4.8% of variance in laying date, in addition to a similarly sized nongenetic effect.

COMMON ENVIRONMENTAL EFFECTS

Resemblance across relatives can—apart from additive genetic effects—also stem from common environmental factors. The common gull pedigree has limited capacity to address the possible covariance across relatives due to common environmental effects, because these are not known for many individuals. We have shown earlier that direct (female) genetic effects on laying date are not affected by maternal effects and effects related to the year of first breeding, and are not subjected to genotype-temperature interactions (Brommer et al. 2008). We here considered whether there is any resemblance across males due to shared temporal environmental effects (year of first breeding and year of birth), and due to shared maternal effects on indirect (male) genetic effects by adding these terms to the final model (model 7, Table 1). There were no temporal effects due to the specific year of when males started to breed (proportion of REML estimated variance explained by year male started to breed: 0.0028 ± 0.0020). The mother and the year of birth (cohort year) were known for 700 males (477 mothers in 35 different birth year). Setting the year of birth for the remaining males as "unknown" revealed that a low proportion of 0.0038 ± 0.0031 of REML estimated variance was explained by year of birth. Coding the unknown mothers as unknown showed little evidence of heterogeneity across mothers (0.0037 ± 0.0041 of REML estimated variance). Because practically all offspring in our study area were ringed, we alternatively assumed that each male whose mother was not known had a different mother because males with unknown mothers originated mainly from other colonies in the whole western Estonian archipelago. This alternative coding produced qualitatively the

Table 3. Annual data on number of pairs identified (breed), the number of recruits produced (n_{rec}), and the linear (β') and nonlinear (γ') standardized selection gradients for survival (surv) and recruitment (rec).

					Females			Males		
Year	breed	n_{rec}	β'_{rec}	γ'_{rec}	surv	β'_{surv}	γ'_{surv}	surv	β'_{surv}	γ'_{surv}
1968	224	22	**−0.64**	**0.29**	192	**−0.08**	0.03	188	−0.01	0.05
1969	206	22	**−0.69**	0.69	175	−0.03	−0.04	181	−0.03	0.05
1970	231	29	**−0.66**	0.39	198	0.01	−0.04	194	0.00	0.00
1971	239	15	**−0.78**	0.31	198	0.01	−0.05	203	0.00	0.04
1972	226	22	**−0.87**	0.48	189	0.01	0.00	200	−0.02	0.03
1973	225	45	**−0.60**	0.17	185	**−0.13**	−0.03	190	0.00	−0.01
1974	190	34	**−0.77**	0.83	166	**−0.06**	0.01	170	0.02	0.00
1975	220	29	**−0.51**	0.17	192	−0.03	−0.01	195	0.03	−0.01
1976	251	23	**−0.80**	0.49	223	**−0.07**	−0.03	220	−0.00	0.04
1977	344	31	**−0.72**	0.40	291	−0.02	0.03	294	−0.04	−0.02
1978	339	11	**−0.92**	0.93	275	−0.04	−0.02	273	−0.03	−0.03
1979	307	18	**−0.86**	0.71	255	−0.05	−0.05	263	**−0.05**	0.00
1980	298	13	**−0.74**	0.57	252	−0.01	−0.01	251	−0.01	0.02
1981	265	47	**−0.53**	**0.07**	228	−0.04	0.02	223	−0.01	−0.00
1982	337	42	**−0.46**	0.12	269	**−0.06**	−0.00	272	−0.04	0.04
1983	315	26	**−0.56**	0.22	158	0.02	−0.13	143	−0.09	−0.12
1986	279	13	**−0.71**	0.52	225	−0.05	**0.09**	239	−0.05	−0.02
1987	335	37	**−0.66**	0.31	284	−0.03	0.00	272	−0.04	0.03
1988	331	65	**−0.40**	**−0.02**	288	**−0.07**	−0.04	266	−0.05	−0.06
1989	344	78	**−0.52**	0.19	278	**−0.07**	0.02	264	**−0.06**	0.01
1990	300	19	**−0.56**	0.11	244	−0.01	0.04	246	−0.04	0.07
1991	317	56	**−0.70**	**0.26**	258	**−0.06**	0.01	257	−0.08	−0.02
1992	362	18	**−0.89**	0.59	306	0.00	−0.04	308	0.02	0.03
1993	343	12	−0.55	0.33	287	−0.01	0.02	292	0.01	0.01
1994	356	28	**−0.69**	0.49	288	−0.03	−0.05	296	0.02	−0.01
1995	338	12	**−0.67**	0.39	276	−0.00	0.03	278	0.01	**−0.08**
1996	371	19	**−0.76**	0.73	296	−0.05	0.03	310	−0.03	−0.02
1997	331	30	**−0.42**	0.02	284	−0.00	−0.03	283	−0.04	0.00
1998	342	36	**−0.35**	0.04	301	**−0.05**	−0.03	309	−0.04	−0.01
1999	340	55	**−0.57**	0.33	309	**−0.08**	−0.03	308	−0.02	0.01
2000	335	39	**−0.68**	**0.79**	303	−0.00	0.00	308	0.02	−0.00
2001	362	62	**−0.57**	0.18	315	0.01	0.01	321	−0.03	−0.00
2002	374	79	**−0.55**	**0.05**	319	0.03	−0.02	328	0.01	−0.01
Average			−0.65	0.37		−0.03	0.00		−0.02	0.00

For females and males, we further present the number of individuals that survived (surv). The sign of the selection gradient is also indicated for very low selection (−0.00). Statistically significant standardized selection gradients are indicated in bold. Significance was based on a generalized linear model with Poisson (for recruitment) or binomial errors (for survival). Average over all years is presented in the last line of the Table, and a sign tests is presented in the main text.

same result. Including any of the common-environmental factors that we could address did not significantly change the male additive genetic effect on female laying date (results not shown) and we therefore conclude that the estimate of male indirect genetic effect is not inflated due to any of these common-environmental factors.

SELECTION

We calculated annual selection on laying date over 33 years (Table 3). There was strong evidence of recruitment selection for earlier laying, as the linear standardized selection gradients were negative in 33 of 33 years ($P < 0.001$), and all but one of the annual linear standardized selection gradients were significant. Nonlinear standardized recruitment selection gradients were positive in 32 of 33 years ($P < 0.001$). The detected nonlinear selection was due to curvature of the fitness map, rather than representing true disruptive selection (Fig. 1). There was evidence of survival selection in females (negative β' in 26/33 years, $P = 0.001$, significantly so in 10 years), but not in males (negative β' in 22/33 years, $P = 0.08$, significant only in two years). Nonlinear

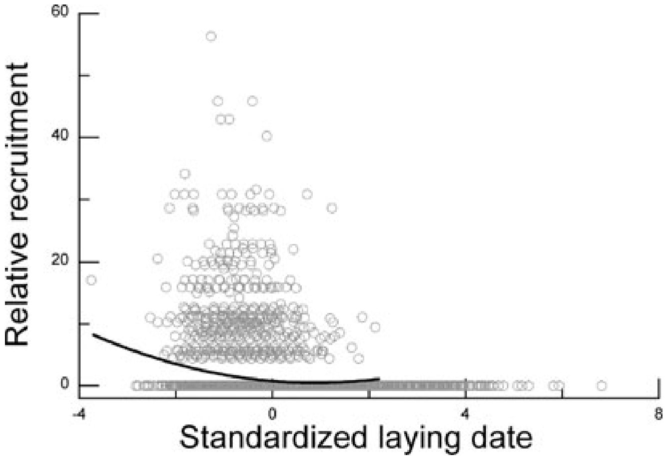

Figure 1. Recruitment selection for laying early in the common gull. Plotted (black thick line) is the function for the average linear and nonlinear standardized selection gradients over 33 years, describing how relative recruitment (observed number of recruits divided by the annual average recruitment) depends on laying date standardized to zero annual mean and unit standard deviation. The plotted line is based on the average annual linear (β') and nonlinear (γ') standardized recruitment selection gradients given in Table 3, where the average constant (expected relative fitness for the mean annual laying date) was 0.77. The average standardized recruitment selection gradient is plotted over the range where relative recruitment is larger than zero. The observed annual data over all 33 years is plotted in gray in the background to aid in visual comparison.

survival selection was absent both in females (negative γ' in 18/33 years, $P = 0.7$), and in males (negative γ' in 16/33 years).

Discussion

Probably one of the most common and important interactions between two unrelated individuals occurs whenever opposite-sex individuals form a pair and reproduce. We have here demonstrated a male indirect genetic effect on the seasonal timing of his partner's reproduction. We have further shown that laying date is a fitness-related trait. Common gulls are under strong and temporally consistent recruitment selection for laying early in the season. Hence, a male's indirect genetic effect on his partner's laying date is clearly evolutionarily relevant. Previous studies on birds that used a mixed model approach to test for female and male-specific effects on avian reproductive traits found that male birds have no significant effect on laying date and clutch size in two species of passerine (Sheldon et al. 2003; McCleery et al. 2004; Gienapp et al. 2006) and one wader species (van de Pol et al. 2006), although male mute swans *Cygnus olor* do have a phenotypic effect on laying date (Charmantier et al. 2006). Evolutionary significant male indirect genetic effects may occur whenever males can contribute to their mate's prereproductive environment, which seems particularly likely to occur in long-lived socially monogamous vertebrates, but may also occur in invertebrates (e.g., where males present a nuptial gift, Gwynne 2008).

Conflict between the sexes is common in nature and, although the genetics of such conflict is currently poorly understood (Arnqvist and Rowe 2005), traits that make a male successful in increasing his partner's reproduction may be generally detrimental in a female. We here find an example of such sexual conflict on the genetic level, where genes for an advancing direct (female) effect on laying date are significantly negatively associated with genes for a delaying indirect (male) effect on laying date. This negative genetic association is probably not due to linkage disequilibrium, because this would require the unlikely scenario of females with genes for early laying consistently pairing with males with genes for an indirect effect of delaying their partner's laying date (and vice versa). Instead, this negative genetic correlation is probably due to antagonistic pleiotropy where genes that advance laying date through a direct effect expressed in females have a delaying effect when expressed in males. The sexually antagonistic genetic effects occur between loci for direct and indirect effect (on the same genome). We know of no other demonstration of such sexually antagonistic genetic effects on a fitness-related trait in the wild. However, negative genetic correlations between direct genetic effects and maternal genetic effects (which are a particular form of indirect genetic effects) are found in several domesticated (Wilson and Reale 2006), and one wild mammal species (Wilson et al. 2005).

We have shown that an animal-model approach allows quantification of the genetics of social interactions between mates, even when the causal male trait affecting his partner's laying date is unknown. The negative genetic correlation between direct (female) and indirect (male) genetic effects may create a force balancing the otherwise temporally consistent selection for earlier laying date in this population. There is increasing evidence for sexually antagonistic genetic effects on fitness traits, which has, apart from a potential role in maintaining genetic variation in the face of selection, also implications for mate choice (Chippindale et al. 2001; Brommer et al. 2007; Foerster et al. 2007). In the common gull, sexually antagonistic genetic effects will reduce the indirect benefits of mate choice for both sexes, because selecting a partner for genes for earlier laying (through either direct or indirect effect) will have antagonistic effects in offspring of the opposite sex. On the other hand, the relatively large nongenetic variance component for the indirect (male) effect suggests that direct (nonheritable) benefits of female mate choice may still be substantial.

In conclusion, we have demonstrated an empirical approach that allows quantification of the genetics of social interactions between mates. Intriguingly, we here find evidence of direct and indirect genetic effects on a fitness-related life-history trait, but also of a significantly negative relationship between these, implying sexually antagonistic genetic effects. Such "hidden" interactions and conflict between mates occurring on the genetic level may be common in nature and may form a considerable evolutionary force, only becoming visible when the traditional evolutionary quantitative genetic framework is expanded to include indirect genetic effects between unrelated individuals.

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