Inbreeding depression in the wild

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Despite its practical application in conservation biology and evolutionary theory, the cost of inbreeding in natural populations of plants and animals remains to a large degree unknown. In this review we have gathered estimates of inbreeding depression (δ) from the literature for wild species monitored in the field. We have also corrected estimates of δ by dividing by F (coefficient of inbreeding), to take into account the influence that the variation in F will have on δ. Our data set includes seven bird species, nine mammal species, four species of poikilotherms (snakes, fish and snails) and 15 plant species. In total we obtained 169 estimates of inbreeding depression for 137 traits; 81 of those estimates included estimates of F. We compared our mammalian data (limited to those traits related to juvenile mortality) to the estimates for captive zoo species published by Ralls *et al.* (1988) to determine if, as predicted from the literature, natural estimates of inbreeding depression are higher than captive estimates. The mean $\delta \pm$ SE (significantly different from zero and not corrected for F) for homeotherms was 0.509 ± 0.081; for poikilotherms, 0.201 ± 0.039; and for plants, 0.331 ± 0.038. Levels of inbreeding depression this high in magnitude will be biologically important under natural conditions. When we limited our data set to mortality traits for mammals and corrected for $F = 0.25$ (as is the case for the Ralls *et al.* data set), we found a significant difference between the two data sets; wild estimates had a substantially higher mean cost of inbreeding at $F = 0.25$: 2.155 (captive species: 0.314). Of the 169 estimates of δ, 90 were significantly different from zero, indicating that inbred wild species measured under natural conditions frequently exhibit moderate to high levels of inbreeding depression in fitness traits.

Keywords: coefficient of inbreeding, fitness, inbreeding depression.

Introduction

Inbreeding depression is the decline in the value of a trait as a direct consequence of inbreeding (Wright, 1977; Shields, 1987). The most common estimates of inbreeding depression involve traits that are closely related to fitness, such as reproductive traits (e.g. number of eggs laid, number of young surviving), or metric traits indirectly associated with fitness (e.g. ejaculate volume, plant height). The reduction of fitness after close inbreeding can be caused by a number of genetic factors: the unmasking of recessive deleterious alleles (Lande, 1994; Lynch *et al.*, 1995), increased homozygosity and/or reduced allozyme variability (Falk & Holsinger, 1991; Brock & White, 1992; Pray *et al.*, 1994; Vrijenhoek, 1994). Whatever the genetic mechanism, inbreeding depression is a real phenomenon that has received a substantial amount of attention in the literature (Ralls & Ballou, 1983, 1986; De Bois *et al.*,

1990; Lacy *et al.*, 1993; see Frankham, 1995a and Roff, 1997 for reviews).

Most of the literature concerning inbreeding depression has concentrated on domestic or captive-bred wild species (Ralls & Ballou, 1986; for a review see Lacy *et al.*, 1993) because of the obvious difficulties of making estimates on wild species in nature. One of the most comprehensive data sets is that of pedigrees from zoo populations (Ralls *et al.*, 1988). Forty captive populations belonging to 38 species show an average increase in mortality of 33% for inbred matings (Ralls *et al.*, 1988). Ralls *et al.* (1988, p. 191) suggest that 'the total costs of inbreeding in natural populations are probably considerably higher', which would make the cost of inbreeding in natural populations of substantial evolutionary consequence. The implications of high levels of inbreeding depression to population extinction are obvious (Lande, 1988; Caro & Laurenson, 1994; Caughley, 1994). However, the degree of inbreeding depression in wild populations remains controversial (see Frankham, 1995a for a discussion). The two most commonly suggested reasons why inbreeding effects in natural populations may not be significant are: (i) animals in the

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wild avoid close inbreeding, and therefore do not manifest the deleterious fitness effects; and (ii) even if inbreeding does occur, animals are able, either behaviourally or physiologically, to deal with the deleterious genetic effects before they are manifest on a phenotypic level, whereas captive species, because of the conditions of captivity, cannot respond in such a manner. Although evidence of inbreeding depression in wild species has been published (see Frankham, 1995a for a short review), the lack of a comprehensive review across species has led to the remaining scepticism about its existence in natural populations (Caro & Laurenson, 1994).

The objective of the present study was to estimate the average inbreeding depression for wild species measured under natural conditions. We are concerned here not with whether inbreeding occurs in the wild (although we report the coefficient of inbreeding, F, for those studies for which it was available) but rather the consequences of inbreeding on characteristics of organisms living in the wild. Specifically, we attempt to answer two questions: (i) is inbreeding depression in wild populations of sufficient magnitude to be biologically important should inbreeding occur? and (ii) does the cost of inbreeding differ between natural and captive populations?

Methods

The data set

We obtained 169 estimates of inbreeding depression from the literature. The data set includes 35 species (20 animals, 15 plants) and 137 traits (see Appendix). We included only species that were sampled from wild populations or species that were artificially inbred in the laboratory, or glasshouse, for one generation and their progeny released, or grown, in the area from which their parents originated. Where more than one estimate was given for a particular trait, we included all estimates in the analysis.

To standardize relative differences in fitness traits, we used the coefficient of inbreeding depression δ (Lande & Schemske, 1985):

$$\delta = 1 - (X_I/X_O),$$

where X_I = inbred trait value and X_O = outbred trait value. To standardize estimates of δ further, we changed traits such as juvenile mortality (where it is expected that $X_O < X_I$) to juvenile survivorship (so that $X_O > X_I$). This way all estimates are 'positive', and the a priori prediction is that outbred values should be greater than inbred ones. Certain traits (e.g. sperm abnormalities in lions) that could not be modified because they were not

expressed as portions of a total, were not used in the analysis. We included traits that were either directly related to fitness, e.g. total number of eggs laid, or traits indirectly related to fitness, e.g. juvenile weight.

Because the magnitude of inbreeding depression will vary with the inbreeding coefficient of the inbred individuals studied, F (Falconer, 1989), we corrected δ estimates by standardizing with respect to F. The change in trait value because of inbreeding is

$$b = (X_O - X_I)/F,$$

where b is the slope of the relationship between trait value and F. Because X_O will vary among traits, we scale by dividing throughout by X_O giving

$$b_{X_O} = (1 - X_I/X_O)/F.$$

Because $1 - X_I/X_O$ is the measure of inbreeding depression, δ, we can simplify the equation to

$$b_{X_O} = \delta/F.$$

Since $\delta = b_{X_O}F$, the standardized slope is equivalent to inbreeding depression when $F = 1$. Therefore, dividing the estimates of δ by F allows for a standardized comparison of the cost of inbreeding. We obtained 81 estimates of F from 14 studies. We called the F-corrected data set b_{X_O} (includes negative values because of $X_O < X_I$).

Statistical analysis

All statistical analyses were carried out using SYSTAT (Wilkinson, 1991). We divided the data set into estimates of δ that were significant and those that were nonsignificant, to determine how often significant levels of inbreeding depression were detected.

To determine if natural conditions increase inbreeding depression relative to captive conditions, we compared the mean inbreeding depression we obtained from the literature with the data set included in the Ralls *et al.* (1988) review of inbreeding depression in captive-bred populations of wild species. Ideally the most appropriate test would be a comparison between natural and captive conditions for the same traits in the same species (paired comparison). We were not able to conduct paired comparisons because of the lack of use of the same species between this and the Ralls *et al.* study. Ralls *et al.* (1988) calculated the slope of ln(survival) vs. inbreeding and then predicted the cost of inbreeding for a level of inbreeding of $F = 0.25$. Because the Ralls *et al.* data set was limited to survival of offspring of mammals only, we limited our data set to traits directly related to

survival in mammals. Our estimates were obtained from the δ data set and corrected for $F = 0.25$. We used a Student's t-test to determine if significant differences exist between mean estimates of the cost of inbreeding at $F = 0.25$ between the two data sets.

Results

Magnitude of inbreeding depression

Theory suggests that females should not mate with their closest relatives unless the cost of inbreeding is less than 0.33 (Smith, 1979). In addition, an increased probability of extinction occurs just below intermediate levels ($F = 0.30–0.40$) of inbreeding (Frankham, 1995b). We found very high mean estimates of inbreeding depression for species measured in the wild. For δ estimates, mean inbreeding depression ranged from 0.197 (poikilotherms) to 0.268 (homeotherms) (Table 1; 30% of estimates > 0.33). In addition, mean ($\pm$SE) δ estimates that were significantly different from zero were 0.509 ± 0.081 for homeotherms, 0.201 ± 0.039 for poikilotherms and 0.331 ± 0.038 for plants. Most of these estimates of inbreeding depression are sufficiently high in magnitude (> 0.33) to be considered biologically important (see Smith, 1979; Frankham, 1995b). In addition, most of the traits (80%), are directly associated with fitness.

For b_{X_O} estimates, mean inbreeding depression corrected for F ranged from 0.552 for plants to 0.818 for homeotherms (Table 1).

Wild and captive comparisons of the cost of inbreeding at F = 0.25

The comparison of our data set (limited to only those inbreeding depression estimates of mortality of mammals and corrected for $F = 0.25$, i.e. $\delta/0.25$) with that of Ralls et al. (1988) revealed a highly significant difference between mean estimates for juvenile mortality (our data set (mean $\pm$ SE): $n = 9$, $\bar{x} = 2.155 \pm 0.482$; Ralls et al. data set: $n = 40$, $\bar{x} = 0.314 \pm 0.044$; $t_{47} = 7.687$, $P = 0.0001$). Even without correcting for $F = 0.25$, our estimate was significantly higher than the Ralls et al.

estimate ($\bar{x} = 0.539 \pm 0.121$; $t_{47} = 2.061$, $P = 0.04$). Although inbreeding depression normally ranges between 0 and 1 (unless the survival of inbreds exceeds that of outbreds), our calculated mean cost of inbreeding of 2.155 results from the correction using $F = 0.25$. As predicted by Ralls et al. (1988), wild estimates of the cost of inbreeding at $F = 0.25$ are substantially higher than captive estimates.

Discussion

We found that statistically significant levels of inbreeding depression in the wild are detected $\approx 54\%$ of the time when species are known to be inbred. When significant, mean inbreeding depression (not corrected for the coefficient of inbreeding, F) ranged from 0.20 in poikilotherms to 0.51 in homeotherms. When corrected for F, mean inbreeding depression for all estimates ranged from 0.55 in plants to 0.82 in homeotherms. The analysis using only mammals revealed significantly greater estimates of the cost of inbreeding at $F = 0.25$ from free-ranging mammals than estimates from captive populations (2.16 and 0.31, respectively). Therefore, as predicted by Ralls et al. (1988), conditions experienced in the wild increase the cost of inbreeding (similar findings have been made for plants; reviewed by Roff, 1997).

Although we have demonstrated that the cost of inbreeding under natural conditions is much higher than under captive conditions, we lack sufficient data to determine which environmental factors cause such an increase. Inbreeding depression is typically more severe in harsher environments (Falk & Holsinger, 1991; Hoffmann & Parsons, 1991; Latter et al., 1995; for a review see Miller, 1994). Environmental factors such as unpredictable rainfall, fluctuating temperatures and limiting resources to feed young are all likely to have a significant effect on juvenile mortality. Weak inbred young that would normally die in the wild would most likely survive in captivity with veterinary assistance (Ralls et al., 1988). Some studies have shown that individuals with relatively low allozyme heterozygosity and/or with a high number of lethal equivalent alleles are much more susceptible to factors that may not affect "normal" individuals (Pierce & Mitton, 1982; O'Brien et al., 1985; Mitton et al., 1986; Murphy et al., 1987; Ralls et al., 1988; Fritz & Simms, 1992; for examples in which no effects are observed see review in Roff, 1997). Although most of our arguments suggest reasons why inbreeding depression will be higher in the wild, inbreeding depression in captivity can be biased upwards as a result of poor husbandry or as an artifact of captive breeding. It has been argued that a reduction in fitness traits is to be expected in animals that have greatly

Table 1 Mean inbreeding depression and standard errors for homeotherms, poikilotherms and plants using the two estimates δ and b_{X_O}

Species group	$\bar{\delta} \pm$ SE	$\bar{b}_{X_O} \pm$ SE	$n\ (\delta)$, $n\ (\bar{b}_{X_O})$
Homeotherms	0.268 ± 0.041	0.818 ± 0.472	63, 20
Poikilotherms	0.197 ± 0.028	0.661 ± 0.121	25, 23
Plants	0.264 ± 0.032	0.552 ± 0.106	75, 34

dissimilar genetic backgrounds (because of the breakdown of coadapted gene complexes), which may be a common occurrence in captive populations (Smith, 1979); in such cases outbreeding depression may have been misdiagnosed as inbreeding depression (Templeton, 1987). The ongoing debate concerning whether the seriously reduced reproductive capacity of cheetahs in captivity is caused by genetic factors or incorrect captive conditions, is a good example of the difficulty of determining the cause of low fitness even for an individual species (Caro & Laurenson, 1994; Merola, 1994; O'Brien, 1994). However, poor husbandry techniques for captive species may increase inbreeding depression, which means that in a situation where an inbred population is maintained under ideal conditions, the inbreeding depression in survival will probably be lower than the Ralls *et al.* (1988) estimate of 0.31, and will be substantially lower than our calculated mean of 0.539.

There are a number of important implications of high levels of inbreeding depression in wild species. Populations that experience high levels of inbreeding and subsequent inbreeding depression may in future generations have significantly lower levels of inbreeding depression even if closely inbred, because of the purging of deleterious recessive alleles expressed during inbreeding (Wright, 1977; Lorenc, 1980; Bryant *et al.*, 1990; Barrett & Charlesworth, 1991; Ribble & Millar, 1992; Hedrick, 1994). Nevertheless, although the expected effects of purging deleterious alleles have been documented to some extent (see Husband & Schemske, 1996 for a review), the degree of purging is questionable (see Frankham, 1995a for a discussion), and an accelerated rate of inbreeding in populations can potentially drive a population towards extinction (Gilpin & Soulé, 1986). Although the susceptibility of most populations of animals and plants to high levels of inbreeding and inbreeding depression is poorly known, our results show that inbred organisms in the wild do exhibit inbreeding depression and that the costs of inbreeding in the wild are substantially higher than previously thought (Ralls *et al.*, 1988). The importance of inbreeding depression for wild populations depends not only on the magnitude of the effect when it occurs but also the likelihood of inbreeding. Although high levels of inbreeding have been observed in some populations of animals and plants (Thornhill, 1993; Husband & Schemske, 1996), much more data are needed to ascertain its frequency.

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Appendix

A list of species, trait type, outbred fitness, inbred fitness values, sample sizes and calculated levels of inbreeding depression for birds, mammals, poikilotherms and plants measured in the wild. Note: X_O = outbred value; X_I = inbred value; outbred n and inbred n are sample sizes; $\delta = 1 - $ (inbred/outbred); Art.? indicates which species were artificially inbred; F = incidence of inbreeding; Sig.? indicates which estimates of outbred fitness values are significantly greater than inbred fitness values; *indicates that the trait type was inappropriate for the analysis (outbred < inbred), could not be modified and therefore was not used; **indicates that the trait was modified from outbred < inbred to outbred > inbred for the analysis. For traits with more than one entry for X_O and X_I, we have calculated a mean δ estimate for the purpose of the Appendix but used individual estimates for the analysis reported in the text

Species	Trait	X_O	Outbred n	X_I	Inbred n	F	δ	Art.?	Sig.?	Reference	Comments
Animals											
Birds											
Accipiter cooperii	Clutch size	4	?	3.7	?		0.075	No	?	Rosenfield & Bielefeldt (1992)	
Aphelocoma ultramarina	Nest success	0.363, 0.510	625	0.344, 0.458	32		0.077	No	No	Brown & Brown (1998)	
	Brood size	3.27	445	2.53	24		0.226		Yes		
	Nestling survival	0.33	858	0.086	35		0.739		Yes		
Geospiza fortis	Clutch size	3.49, 3.57	27, 8	3.50, 3.34		0.085, 0.125	0.031	No	No	Gibbs & Grant (1989)	Total sample size
	No. eggs hatched	2.01, 1.92	27, 8	1.65, 1.68		0.085, 0.125	0.152		No		
	No. young fledged	1.67, 1.58	27, 8	1.40, 1.52		0.085, 0.125	0.1		No		
	No. young surviving	0.69, 0.77	16, 6	0.52, 0.72		0.085, 0.125	0.155		No		
	% eggs hatched	54, 51	27, 8	45, 44		0.085, 0.125	0.152		No		
	% young fledged	79, 79	21, 6	85, 75		0.085, 0.125	−0.013		No		
	% eggs fledged	45, 41	27, 8	38, 36		0.085, 0.125	0.139		No		
	% young surviving	48, 51	14, 5	33, 39		0.085, 0.125	0.274		No		
Geospiza magnirostris	Hatching success	0.84	?	0.73	?	0.092	0.173	No	No	Grant & Grant (1995)	
	Fluctuating asymmetry	−0.068	41	2.33		0.092	?		Yes		Total sample size
Malurus splendens	Number of nests	127	107	47	29		0.63	No	?	Rowley *et al.* (1986)	No. breeding pairs
	Number of eggs	378	107	142	29		0.62		?		
	Number of nestlings	336	107	125	29		0.63		?		
	Number of fledglings	301	107	109	29		0.64		?		
	Number of yearlings	115	107	46	29		0.6		?		
	Clutch size	3	107	3	29		0		No		
	Clutches/year/female	1.7	107	1.8	29		−0.06		No		
	Nestlings/eggs	0.89	107	0.88	29		0.01		?		
	Fledglings/nestlings	0.9	107	0.87	29		0.03		?		
	Yearlings/fledglings	0.38	107	0.42	29		−0.11		No		
	Nestling survival	79.7	107	76.8	29		0.04		No		
Melospiza melodia	Reproductive success	0.13	136	−0.18	8		?	No	No	Arcese (1989)	
Melospiza melodia	Survival	135, 95	230	30, 5	35		0.863	No	Yes	Keller *et al.* (1994)	

Species	Trait								Reference	
Parus major	% fledging survival	82.5	?	62	68	0.248	No	?	Bulmer (1973)	
Parus major	% survival after fledging	7.8	?	0	42	1		Yes		
Parus major	Clutch size	8.38	13	8		0.045	No	No	Greenwood *et al.* (1978)	Total sample size
Parus major	% nestling survival**	83.8	15	72.3		0.137		Yes		Total sample size
Parus major	% fledging recovery	10	9	5.8	5	0.42		No		
Parus major	Hatching success I**	0.963	8	0.8	13	0.169	No	Yes	Van Noordwijk & Scharloo (1981)	
	Hatching success II**	0.851	8	0.679	13	0.202		Yes		
	Brood success**	0.779	8	0.634	13	0.186		No		
	Fledging survival	14.5	?	16	?	−0.103		No		
Mammals										
Acinonyx jubatus	Juvenile survivorship**	73.7	519	55.8	?	0.243	No	?	O'Brien *et al.* (1985)	
Cynomys ludovicianus	Probability producing litter	0.51	253	0.5	6	0.02	No	No	Hoogland (1992)	
	Litter size	3.16	147	3	3	0.051		No		
	Juvenile weight	152	148	148	4	0.026		No		
	No. emergent young	1.53	146	1.33	3	0.131		No		
	% emergent young	49	146	67	3	−0.367		No		
Leontopithecus rosalia	No. offspring surviving	0.829	175	0.474	38	0.428	No	Yes	Dietz & Baker (1993)	
	% reproductive success	86	5	0	14	1		Yes		
Panthera leo	Ejaculate volume	9.4	8	5.9	8	0.372	No	Yes	Wildt *et al.* (1987)	Serengetti Park vs. Sakkarbaug Zoo
	Sperm motility	91	?	61	?	0.33		Yes		
	Sperm per ejaculate	34.4	?	13.3	?	0.613		No		
	Motile sperm/ejaculate	228.5	?	45.3	?	0.802		Yes		
	Total sperm abnormalities*	24.8	?	66.2	?	−1.669		Yes		
Papio anubis	% offspring viability	84.2	38	50	8	0.406	No	Yes	Packer (1979)	
Papio cynocephalus ursinus	% infant survival/30d.	4	27	0	20	1	No	No	Bulger & Hamilton (1988)	
Papio cynocephalus	% offspring survival	81	140	0	3	0.06	1	No	Yes	Alberts & Altmann (1995)

Appendix (*Continued*)

Species	Trait	X_O	Outbred n	X_I	Inbred n	F	δ	Art.?	Sig.?	Reference	Comments
Peromyscus leucopus nov.	% survivorship**	100	67	56	56	0.25	0.44	Yes	Yes	Jimenez *et al.* (1994)	
Sorex araneus	Body mass	21.4	207	21.8	159	0.25	−0.019		Yes	Stockley *et al.* (1994)	
	Offspring survival	0.35	28	0.28	?		0.2	No	Yes		
Poikilotherms											
Arianta arbustorum	No. of clutches	17	8	13.6	7	0.25	0.2	Yes	No	Chen (1993)	
	Clutch size	19.7	8	17.2	7	0.25	0.127		No		
	No. of eggs	313.9	8	244.6	7	0.25	0.221		No		
	Hatching success	0.485	8	0.304	7	0.25	0.373		Yes		
	No. hatchlings	164.6	8	73	7	0.25	0.557		Yes		
	No. dead embryos*	40	8	22.14	7	0.25	0.447		No		
	Reproductive success**	0.5	8	0.33	7	0.25	0.34		Yes		
	Proportion surviving	0.8	8	0.58	7	0.25	0.275		Yes		
Salmo gairdneri	% survival of eyed eggs	95.1, 94.6, 96.8	100, 100, 100	86.2, 79.3, 91.0	100, 100, 100	0.25, 0.375, 0.5	0.1	Yes	Yes	Gjerde *et al.* (1983)	
	% survival of alevins	99.0, 98.4, 96.3	100, 100, 100	96.2, 90.1, 91.5	100, 100, 100	0.25, 0.375, 0.5	0.053		Yes		
	% survival of fry	81.4, 72.7, 72.6	100, 100, 100	72.3, 67.1, 54.0	100, 100, 100	0.25, 0.375, 0.5	0.111		Yes		
	Growth of fingerlings	12.0, 47.8, 12.2	100, 100, 100	10.8, 37.0, 12.7	100, 100, 100	0.25, 0.375, 0.5	0.094		No		
	Growth of adults	2.50, 3.15, 2.96	100, 100, 100	2.22, 2.52, 2.05	100, 100, 100	0.25, 0.375, 0.5	0.21		No		
Salmo salar	Recapture frequency	0.052	351	−0.418	44	0.25	?	Yes	Yes	Ryman (1970)	No. of families
Vipera berus	Brood size**	10	10	7	10		0.3	No	Yes	Madsen *et al.* (1996)	
	% viable offspring**	91	?	68.4	?		0.248		Yes		
Plants											
Chamaecrista fasciculata	% fruit maturation	0.5	?	0.45	?		0.1	Yes	No	Fenster (1991)	Selfed vs. farthest outcrossing neighbour
	% seed germination	0.35	?	0.3	?		0.143		No		
	Flower production/plant	8	?	4	?		0.5		Yes		
	No. seeds/fruit	10.5	?	9.4	?		0.105		Yes		
	% survival	0.44	?	0.3	?		0.318		No		
	Fruit production/plant	1.6	?	0.65	?		0.594		No		
	Progeny fitness	0.6	?	0.13	?		0.783		Yes		
Costus allenii	Seed production	46.7	62	30.5	67	0.5	0.35	Yes	Yes	Schemske (1983)	
	No. seeds germinated	96, 9	300, 300	94, 10	300, 300	0.5	−0.04		No		
	No. seedlings surviving	10, 0	300, 300	12, 0	300, 300	0.5	−0.1		No		
Costus laevis	Seed production	52.9	44	26.2	45	0.5	0.5	Yes	Yes	Schemske (1983)	
	No. seeds germinated	130, 10	300, 300	109, 11	300, 300	0.5	0.03		No		

Character						δ			Reference
									Total sample size
									Sample size not exact
Costus guanaiensis									
No. seedlings surviving	12, 0	300, 300	11, 0	300, 300	0.5	0.04		No	Schemske (1983)
Seed production	107.9	54	81.2	57	0.5	0.25	Yes	Yes	Schemske (1983)
Delphinium nelsoni									
Seeds per flower	15, 16, 10, 13	1016	10, 9, 5, 0		0.5	0.573	Yes	Yes	Price & Waser (1979)
Seedling survival	0.159, 0.071	145, 98	0.052, 0	58, 98	0.5	0.837		Yes	
Erythronium americanum									
% fruit production	75	32	33.3	30	0.5	0.556	Yes	Yes	Harder *et al.* (1985)
Gilia achilleifolia									
Seed production	41.2	23	10.5	7	0.5	0.745		Yes	
Average seed mass	3.6	22	3.8	5	0.5	−0.056		No	
% seeds not aborted**	96.9		97.1			−0.002	Yes	No	Schoen (1983)
% seed germination	55.4		85.7			−0.55		Yes	
% seedling establishment	100		69			0.31		Yes	
% survival	0.5		0.25			0.5		Yes	
Average seed production	6.69		7.53			−0.126		No	
No. capsules per plant	5.51		4.18			0.241		No	
Relative fitness	1		0.57			0.43		No	
Ipomopsis aggregata									
Seed size	1.58, 1.50	100	1.44, 1.21	100		0.141	Yes	Yes	Heschel & Paige (1995)
Germination success	38.32, 38.57	100	27.88, 22.68	100		0.342		Yes	
% survival**	87.5	100	71.2	100		0.186		Yes	
Final height	27.4	100	23.6	100		0.139		Yes	
Linnanthes alba									
No. flowers per plant	58.3, 58.2, 63	21, 34, 32	50.1, 50.9, 58.8	35, 61, 42		0.11	No	Yes	Jain (1978)
Plant height	22.1, 20.7, 19.9	21, 34, 32	18.3, 18.5, 18.7	35, 61, 42		0.11		Yes	
Seed per flower	1.08, 0.9, 0.77	21, 34, 32	0.50, 0.53, 0.54	35, 61, 42		0.42		Yes	
Lobelia cardinalis									
% survival**	100	186	54	141		0.46	Yes	No	Johnston (1992)
Flower number**	100	163	55	126		0.45		No	
% flowering**	100	186	47	143		0.53		Yes	
Net fertility**	100	?	29	?		0.71		Yes	
Lobelia siphilitica									
Flower number**	100	93	71	57		0.29	Yes	Yes	Johnston (1992)
Net fertility**	100	?	46	?		0.54		Yes	
Lolium multiflorum									
Heading date*	15.56	?	18.32	20		−0.177	Yes	Yes	Polans & Allard (1989)
Tiller height	108.27	?	91.96	20		0.151		Yes	
No. spikelets	38.8	?	33.85	20		0.128		Yes	
Glume length	12.52	?	11.22	20		0.104		Yes	
No. tillers	220.22	?	173.59	20		0.212		Yes	
Seed weight	2.9	?	2.88	20		0.007		Yes	

Appendix (*Continued*)

Species	Trait	X_O	Outbred n	X_I	Inbred n	F	δ	Art.?	Sig.?	Reference	Comments
Sabatia angularis	% progeny survival	68	1348	50	?	0.5	0.265	Yes	Yes	Dudash (1990)	
	Total fruit mass	98	1143	40	?	0.5	0.592		Yes		
	Relative progeny fitness	99	?	25	?	0.5	0.747		Yes		
	Seed number per fruit	834	25	730	25	0.5	0.125		Yes		
	Seed mass/fruit	0.023	25	0.022	25	0.5	0.043		No		
Sidalcea oregana	% seeds germinated	14.01	147	13.47	72	1	0.039	Yes	No	Ashman (1992)	
	Juvenile growth rate	0.0277	75	0.0324	21	1	−0.17		No		
	% seedling survival	67	445	59	?	1	0.119		No		Total sample size
	% offspring reproductive	49.5	658	46.5		1	0.061		No		Total sample size
	Plant size	140	16	80	12	1	0.429		Yes		
	No. flowers produced	54	80	40		1	0.259		Yes		Total sample size
	Multiplicative fitness	0.074	18	0.06	11	1	0.189		No		
Zostera marina	Seed set	0.437, 0.273	336	0.306, 0.217	330	0.5	0.253	Yes	Yes	Ruckelshaus (1995)	
	Mean fitness	1.0, 1.0	336	0.7, 0.795	330	0.5	0.253		Yes		