Haldane's rule revisited: do hybrid females have a shorter lifespan? Survival of hybrids in a recent contact zone between two large gull species

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Abstract

Haldane's rule predicts that particularly high fitness reduction should affect the heterogametic sex of interspecific hybrids. Despite the fact that hybridization is widespread in birds, survival of hybrid individuals is rarely addressed in studies of avian hybrid zones, possibly because of methodological constraints. Here, having applied capture–mark–recapture models to an extensive, 19-year-long data set on individually marked birds, we estimate annual survival rates of hybrid individuals in the hybrid zone between herring (*Larus argentatus*) and Caspian (*Larus cachinnans*) gulls. In both parental species, males have a slightly higher survival rate than females (model-weighted mean ± SE: herring gull males 0.88 ± 0.01, females 0.87 ± 0.01, Caspian gull males 0.88 ± 0.01, females 0.87 ± 0.01). Hybrid males do not survive for a shorter time than nonhybrid ones (0.88 ± 0.01), whereas hybrid females have the lowest survival rate among all groups of individuals (0.83 ± 0.03). This translates to a shorter adult (reproductive) lifespan (on average by 1.7–1.8 years, i.e. ca 25%) compared with nonhybrid females. We conclude that, in line with Haldane's rule, the lower survival rate of female hybrids may contribute to selection against hybrids in this hybrid zone.

Introduction

The Bateson–Dobzhansky–Muller model predicts that when incompatible alleles, which have evolved in allopatry, meet in a secondary contact zone, their interaction may lead to fitness reduction (Price, 2008). Moreover, the heterogametic sex of the F_1 offspring should experience a higher fitness reduction if the recessive alleles are located on the sex chromosomes; this is known as Haldane's rule (Haldane, 1922; Orr, 1997). According to this rule, reduced fitness of the heterogametic sex in hybrid individuals seems to be an important mechanism of speciation in a variety of organisms (Coyne & Orr, 2004). For example, in the hybrid zone between pied *Ficedula hypoleuca* and collared *F. albicollis* flycatchers, F_1 hybrid females, which

represent the heterogametic sex in birds, are completely sterile and F_1 hybrid males have a much lowered fertility (Svedin *et al.*, 2008). The strength of post-zygotic isolation is even more evident in the long-term perspective, that is, over multiple generations (Wiley *et al.*, 2009). Reduced female-mediated gene flow between species as compared to male-mediated flow has been reported in large gulls (the genus *Larus*) and eagles (*Aquila*) (Crochet *et al.*, 2003; Helbig *et al.*, 2005; Backström & Väli, 2011), this being attributed to the reduced fitness of female hybrids in line with Haldane's rule.

Hybrid fitness relative to the parental species, combined with the frequency of hybridization, determines the introgression rates in hybrid zones (Borge *et al.*, 2005) and is of primary importance in maintaining hybrid zones. One crucial component of fitness is the number of fledged offspring produced during a lifetime, which is directly linked to individual lifespan, which in turn depends on annual survival probability. Svedin *et al.* (2008) showed that the average lifespan of hybrid flycatchers was no different from that of either parental species, and in Darwin's finches, interspecific hybrids

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actually survived better than the parental species (Grant & Grant, 1996, 2010), but for most other avian hybrid zones, we lack such knowledge. The survival of hybrids is of primary importance for shaping the relative fitness of hybrids, for introgression and the persistence of the whole hybrid zone. However, differences in survival between hybrids and parental species under natural conditions may easily go undetected or may be misinterpreted as unimportant, despite the fact that they translate to moderate or large differences in lifespan. The survival of animals in wild populations is hardly ever known with 100% confidence. Its estimation is methodologically difficult because it requires the long-term study of uniquely marked individuals (Lebreton *et al.*, 1992), whereas most studies of avian hybrid zones are based on short-term surveys or even single sampling events across the zone. In consequence, although in admixed populations hybrids are typically less abundant than expected from mating frequencies, which indicates selection against hybrids (Helbig *et al.*, 2001, 2005; Veen *et al.*, 2001; Svedin *et al.*, 2008), most studies either only hypothesize about possible reasons or attribute the observed low frequency of hybrids to some post-zygotic isolation. The general gap in knowledge about the survival of hybrids may blur our understanding of the relative importance of particular pre- and post-zygotic barriers, and thus, the true nature of hybrid disadvantage.

Apart from reduced hybrid survival, post-zygotic barriers limiting the numbers and reproductive output of hybrids include mechanisms of sexual selection, that is, low mating and breeding success (Price, 2008). For instance, in hybridizing flycatchers, male hybrids experience fitness reduction through decreased mating success and the increased probability of being cuckolded, whereas female hybrids are sterile (Veen *et al.*, 2001; Svedin *et al.*, 2008). In general, lower mating success may result from the development of intermediate and therefore less attractive phenotypic traits (plumage, song, other courtship displays; Price, 2008). Alternatively, hybrids, with their intermediate phenotype, may be less successful in establishing and holding good-quality territories or may be unable to use parental niches (Grant & Grant, 1997a; Hartfield & Schluter, 1999; Naisbit *et al.*, 2001). It is usually a combination of some of the above-mentioned hybrid characteristics that affects their fitness (Price, 2008; Svedin *et al.*, 2008). Recently, Wiley *et al.* (2009) have shown that post-zygotic isolation might be severely underestimated if one considered only the reproductive output of F_1 hybrids when assessing hybrid fitness.

In this study, we focus on the survival probability of hybrid individuals from the recent secondary contact zone of herring (*Larus argentatus*) and Caspian (*Larus cachinnans*) gulls. These two closely related species hybridize across the central-eastern European lowlands, notably in Poland (Neubauer *et al.*, 2006, 2009; Gay

et al., 2007; Zagalska-Neubauer & Neubauer, 2012). So far, the body of evidence regarding hybrid fitness in this contact zone is equivocal. On the one hand, clutch size is affected only by the body mass of the breeding female and not by the species; on the other hand, hatching success is clearly affected by pair composition and tends to be the lowest in pairs containing hybrids (Zagalska-Neubauer & Neubauer, 2012). Besides, the body mass of hybrid females is not significantly lower than that of females of the parental species (Zagalska-Neubauer & Neubauer, 2012). Here, we test whether, in concordance with Haldane's rule, female hybrids have a lower survival probability compared with females of the parental species and compared with males. If this hypothesis is true, we are further interested in assessing the magnitude of the difference in survival rates among the target groups of birds. To address the above questions, we analyse extensive capture–mark–recapture (CMR) data collected for the two parental species and their hybrids from a 19-year survey in the contact zone in central Poland.

Materials and methods

Study species

The herring gull and Caspian gull are large gregarious waterbirds, widespread in Europe. Both species are similar in size, plumage and breeding ecology. The breeding range of the herring gull includes coastlines and, following its recent expansion, also inland sites. The Caspian gull is a more inland species, as it originally bred in steppe lakes in western Asia, but it can also breed along coasts (Malling Olsen & Larsson, 2004). Both species have expanded their ranges to meet and hybridize in a secondary contact zone in the European lowlands (Neubauer *et al.*, 2006; Gay *et al.*, 2007), where the pre- and post-zygotic reproductive barriers identified so far are relatively weak. They involve positive assortative mating (i.e. mixed pairings are less frequent than expected by chance), best explained by the differential breeding phenology and mate choice based on bare-part colouration (Neubauer *et al.*, 2009; Zagalska-Neubauer & Neubauer, 2012).

Study site and data collection

The studied colony is situated by the dam of the Włocławek Reservoir on the River Vistula in central Poland; it has already been described in detail (Zagalska-Neubauer & Neubauer, 2012). The colony has been monitored since its establishment in 1985 (M. Zieliński, P. Zieliński, M. Lamentowicz & J. Pietrasik, unpublished data). In this study, we use the data from a 19-year period (1990–2008), during which monitoring of these birds was relatively intensive.

Capture–recapture data come from the trapping of nesting adults, and intensive visual observations

performed annually. Trapping was performed on randomly chosen nests with walk-in traps placed over the nests between mid-April and late May each year. Each trapped bird was ringed with uniquely coded colour rings and released. From 2002 onwards, a blood sample was additionally taken from the majority of trapped individuals, to be used for their genetic assignment (see Gay *et al.*, 2007). Visual observations were based on the systematic scanning of territorial birds early in the season (April-early May) and reading off their coloured rings using a 20–60× zoom scope. In all, our CMR data contained records of 399 adults, 278 of which were observed in more than 1 year. For further details of the fieldwork protocols, see Gay *et al.* (2007), Neubauer *et al.* (2009) and Zagalska-Neubauer and Neubauer (2012).

Species assignment and sex identification

Visually, hybrids between herring and Caspian gulls are relatively easily identified in the field as they exhibit an intermediate phenotype, although proper identification does require careful examination of a few most important traits (Gibbins *et al.*, 2011). At first capture, each bird was assigned to one of three predefined categories: herring gull, intermediate (hybrid) or Caspian gull with the use of reference samples from the core ranges. As in our previous studies (Gay *et al.*, 2007; Neubauer *et al.*, 2009), the reference samples for phenotypic assignment included adult birds (trapped and ringed) from the core ranges of both hybridizing species: the Sea of Azov for pure Caspian gull ($N = 55$) and the Baltic Sea for pure herring gull ($N = 32$). Based on the six most divergent phenotypic traits between the two species, principal components were obtained with the use of PCA in Statistica 6.0 (StatSoft, 2003); individuals whose scores fell outside the 95% confidence intervals around means of PC1 distributions in allopatric populations were classified as intermediate (hybrid) individuals (see Zagalska-Neubauer & Neubauer, 2012). Wherever possible, species classification was additionally facilitated by Bayesian genetic assignment based on nine microsatellite loci and performed in STRUCTURE (see Gay *et al.*, 2007). Reference genetic samples from the core range included Caspian gulls from the Sea of Azov ($N = 30$) as well as herring gulls from the Baltic Sea ($N = 50$) and Norway ($N = 8$). Phenotypic and genotypic assignment methods show high consistency and allow for reliable identification of birds based on phenotypic traits alone (Gay *et al.*, 2007). It should be noted that the hybrid group most likely includes F_2 and backcross hybrids, as they are inseparable from F_1 hybrids. However, using pedigree data, Gibbins *et al.* (2011) have shown that adult F_1 hybrids are fairly uniform and phenotypically intermediate between parental species, and the known F_2 hybrid was also intermediate when mature (apart from this, F_2 hybrids should be

very rare as expected from pairing frequencies – pairs consisting of two hybrid individuals represent about 4% of all pairs in the population studied, Zagalska-Neubauer & Neubauer, 2012). Backcross hybrids are expected to be more similar to parental species in phenotype, but the rather conservative assignment method used here prevents the assignment of individuals with such a phenotype into pure species groups.

Sex determination followed the discriminant function developed for this mixed population and was robust to interspecific differences (Neubauer & Zagalska-Neubauer, 2006); it was checked using a subsample of individuals sexed with molecular markers (Griffiths *et al.*, 1998). Again, molecular and morphological sexing agreed in all the individuals tested with both methods ($N = 149$).

Survival analysis

The CMR data were analysed with MARK 5.1 software (White & Burnham, 1999). We applied Cormack–Jolly–Seber type constrained models, which allow the likelihood of different patterns in survival φ and capture probability P to be assessed (Schwarz & Arnason, 1996; Schwarz & Seber, 1999). The patterns evaluated included the constant value of either φ or P across all the years and individuals, the annual variation of these parameters and their differences for groups of individuals. Among the latter, we tested the effects of species, sex and hybrid status (i.e. parameter value in a hybrid group different from that of a nonhybrid group) in various combinations.

The performance of all the models was compared using the Akaike information criterion corrected for small sample size (AIC_c) (Akaike, 1973; Hurvich & Tsai, 1989). Based on AIC_c values, we obtained the Akaike weight of each model, which should be interpreted as the probability of the model being the most appropriate one (Burnham & Anderson, 2001). Subsequently, we calculated the cumulative weight of models including a particular effect (annual variation, species, sex, hybrid status in both sexes, hybrid status only in females, hybrid status only in males) to evaluate their relative importance for survival and capture probability. The above procedure closely follows the approach suggested by Johnson and Omland (2004; see this reference for its full rationale), which has been recently gaining in popularity in ecological studies involving analyses of phenomena influenced by multiple factors (cf. Beck & Fiedler, 2009; Nowicki *et al.*, 2009).

We estimated mean survival in male and female herring and Caspian gulls and hybrids of both species as the weighted mean (with Akaike weights applied) of the survival estimates yielded by the models that could be considered at least partly supported by the data, that is, those with AIC_c differing in value from the minimal one by < 7 (Burnham & Anderson, 2001). All the supported

models showed a relatively good fit as indicated by goodness-of-fit test results (bootstrap GOF *P* between 0.221 and 0.435). It must be stressed that the inclusion of further models changed the weighted mean survival estimates very little other than their slightly lower precision. The mean adult life span in each group was derived from the mean survival as $\hat{e} = (1 - \hat{\varphi})^{-1} - 0.5$ (Nowicki *et al.*, 2005).

Results

Among the Cormack–Jolly–Seber type constrained models applied to explain the patterns in survival and capture probability of adult gulls, the model with annual variation in both parameters as well as the effects of sex and female hybrid status on survival was clearly the best-supported one (Akaike weight exceeding 33%; Table 1). In other words, the model assumed that gull survival not only fluctuated across years, but also differed between males and females, and furthermore among females, it differed between hybrid and nonhybrid individuals. It should be noted that the aforementioned group effects were additive to annual variation, that is, survival estimates varied across years and differed among groups, but the intergroup differences remained consistent across years. The same is true for the patterns in both survival and capture probability in all the models presented in Table 1.

Annual variation proved to be the decisive factor affecting gull capture probability, with its cumulative Akaike weight across all the models tested exceeding 99%, whereas the impact of any group effects was negligible, indicating similar probabilities of capture, regardless of species (Table 2). The fluctuations of capture probabilities across years showed no particular pattern, with the minimum of 0.12 ($\pm$ SE = 0.03) in 2001 and the maximum 0.77 ($\pm$ SE = 0.04) in 2007 apparently reflecting variation in sampling intensity. In the case of survival, annual variation was again the most crucial driver, but sex and female hybrid status also played important roles. Their cumulative Akaike weights were well above 50%, which implies that the presence of both effects is more likely than their absence. On the other hand, there was little indication of gull survival depending on species or being influenced by hybrid status in males.

Consistently with the above findings, the mean annual survival rate was the highest and almost identical for all groups of males (0.882–0.883 with SE = 0.011

Table 2 Relative importance of factors affecting survival and capture probability in adult gulls, represented by the cumulative Akaike weight of models containing a given factor.

Factor	Effect on model parameters	
	Survival	Capture probability
Annual variation	0.958	0.997
Species	0.019	0.033
Sex	0.718	0.191
Hybrid status in females	0.656	0.159
Hybrid status in males	0.166	0.136
Hybrid status in both sexes	0.151	0.126

Table 1 Performance of the supported Cormack–Jolly–Seber type constrained models applied to the estimation of survival and capture probability in adult gulls (*Larus argentatus*, *L. cachinnans* and hybrids of both species). The models are listed in the order of decreasing support, as indicated by Akaike's information criterion corrected for small sample size (AIC$_c$) and Akaike weight. All the other models (not shown) performed worse, with their Akaike weights considerably below 1%.

Model description							
Patterns in survival		Patterns in capture probability					
Annual variation	Group effects	Annual variation	Group effects	AICc	Akaike weight	Number of parameters	Deviance
Yes	Sex; hybrid status in females	Yes	None	2940.74	0.335	38	1455.03
Yes	Sex	Yes	None	2942.58	0.133	37	1363.19
Yes	Sex; hybrid status in both sexes	Yes	None	2943.81	0.072	39	1548.98
Yes	Sex; hybrid status in females	Yes	Sex; hybrid status in females	2944.08	0.063	40	1453.08
Yes	Hybrid status in females	Yes	None	2944.1	0.062	37	1224.42
Yes	Sex	Yes	Sex	2944.32	0.056	38	1362.78
Yes	Hybrid status in females	Yes	Hybrid status in both sexes	2945.31	0.034	38	1223.49
Yes	Hybrid status in both sexes	Yes	Hybrid status in both sexes	2945.5	0.031	38	1291.93
Yes	None	Yes	Hybrid status in both sexes	2945.57	0.03	37	1294.14
Yes	Hybrid status in both sexes	Yes	None	2946.44	0.019	37	1295.01
Yes	None	Yes	Species	2946.74	0.017	38	1470.98
Yes	None	Yes	Sex; hybrid status in females	2946.78	0.016	38	1460.08
Yes	Species, sex	Yes	None	2947.56	0.011	41	1359.58

to 0.012; Fig. 1a). The estimates for both herring and Caspian gull females were slightly lower (0.871–0.872, SE = 0.010–0.012), while hybrid females experienced substantially decreased annual survival (0.833, SE = 0.029; Fig. 1a). The differences in survival that we recorded translate into considerable differences in adult lifespan. Nonhybrid females lived almost 1 year shorter than males (7.2–7.3 vs. 7.9–8.1 years), and the lifespan of hybrid females was further reduced by over one and a half years to ca 5.5 years (Fig. 1b).

Discussion

In our study, we focused on modelling and estimating the annual survival of hybrids and parental, hybridizing species in the secondary contact zone between two large gulls. There have been just a few earlier attempts to do so directly in birds, including studies of interspecific hybrids of Darwin's finches (Grant & Grant, 1997a, b, 2010) and flycatchers (Svedin *et al.*, 2008; Wiley *et al.*, 2009). This low number of studies is mostly due to the difficulty of tracking the fate of usually infrequent hybrid individuals over the years. None of the

Fig. 1 Mean survival (a) and life span (b) of adult gulls (dark bars: *Larus argentatus*, light bars: *Larus cachinnans*, striped bars: hybrids of both species). The whiskers represent 95% confidence intervals.

aforementioned research used CMR methodology applied to the long-term data of marked birds, including hybrid individuals.

The estimates of survival probability presented in this article are similar to other estimates published for herring gulls from both Europe (e.g. Coulson & Butterfield, 1986; Pons & Migot, 1995; Allard *et al.*, 2006; Rock & Vaughan, 2013) and North America (e.g. Allard *et al.*, 2006; Breton *et al.*, 2008), as well as those for other similar-sized gull species (e.g. Spear *et al.*, 1987; Reid, 1988; Pugesek *et al.*, 1995; Altwegg *et al.*, 2007). No survival estimates for Caspian gulls have been published so far, but given its similarity to herring gull, the annual survival of this species not surprisingly falls within the frequently noted range in large gulls, that is, between 0.8 and 0.9.

The adult survival probability of a long-lived species strongly affects population dynamics and, together with fecundity, determines population trends (Caswell, 2001). The difference between survival probability estimates we report in this article and the resulting differences in life span are evident. Hybrid females lived and reproduced, on average, 1.7–1.8 years shorter than females of both parental species, which means a reduction in the reproductive (adult) life span by approximately 25% compared with females of the parental species.

The application of Cormark–Jolly–Seber models means that – as in all studies using this model type – mortality and emigration cannot be distinguished, and consequently, the estimated parameters represent residence rates rather than survival. This might have affected our results if site fidelity was considerably lower in female hybrids than in other groups. However, breeding dispersal is generally rare in large gulls (Greenwood & Harvey, 1982). Earlier studies of herring gulls and related taxa reported their high apparent survival, with no intersexual differences (see, e.g. Pons & Migot, 1995; Allard *et al.*, 2006; Breton *et al.*, 2008 and references therein). Both sexes display strong site fidelity, and their dispersal usually happens only as a result of a failure to breed or mate change (Greenwood & Harvey, 1982, unpublished data). In line with this, we observed that many birds – both parental species and hybrids – were resident breeders for ten or more seasons in a row. This indicates that the rarity of breeding dispersal holds true at our study site as well. Consequently, there is little chance that dispersal substantially affected the estimates of survival in the present study. Apart from this, there are no reasons for expecting that the emigration rate would be particularly higher in female hybrids; we therefore assumed emigration to have little effect on the outcome of our analysis.

Several prezygotic isolation mechanisms are known to reduce the production of hybrid individuals in secondary contact zones. Assortative mating reduces the likelihood of heterospecific pairing, which is also the
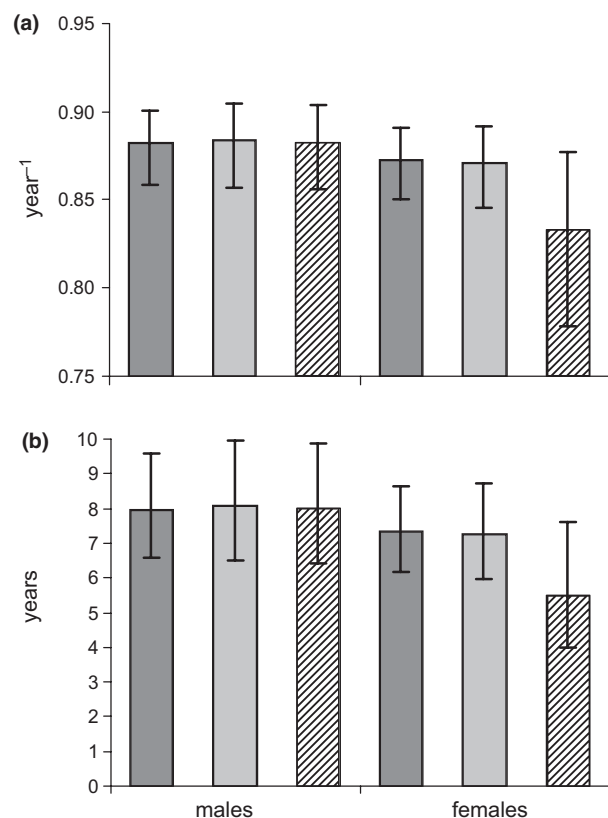
case in the gull hybrid zone studied here (Neubauer *et al.*, 2009). When formed, heterospecific pairs may experience lower breeding success, so that fewer hybrid offspring are produced compared with conspecific pairs. This may arise, for example, when fertilization success or the development chances of embryos are reduced (Price & Bouvier, 2002; Price, 2008). Then, females in heterospecific pairs may avoid producing hybrid offspring by engaging in extra-pair copulations with conspecifics, as found in flycatchers (Veen *et al.*, 2001; Wiley *et al.*, 2007, 2009). However, this was not the case in two other studies focusing on this issue. In the chickadee (*Poecile atricapillus* and *P. carolinensis*) hybrid zone, females in genetically dissimilar pairs were no more likely to engage in extra-pair fertilizations (Reudink *et al.*, 2006), while in hybridizing warblers (*Vermivora pinus* and *V. chrysoptera*) extra-pair paternity was even considered to increase hybridization frequency (Vallender *et al.*, 2007). When hybrids are produced, post-zygotic isolation may include their lowered mating success, defined as establishing a breeding territory and finding a mate, for example, because of their intermediate phenotype, song or other courtship displays (Price, 2008). Lower breeding success could further occur following the cuckolding of a hybrid (Svedin *et al.*, 2008). In addition to the aforementioned mechanisms, the poorer survival of hybrids addressed in the present study, which translates into a shorter adult lifespan and most likely results in a smaller number of offspring produced during a lifetime, may further limit numbers of hybrids in admixed populations.

Hybrids are frequently less numerous than expected in avian hybrid zones (e.g. Saino & Bolzern, 1992; Saino & Villa, 1992; Helbig *et al.*, 2001, 2005). Under the assumption of a closed population and equal fitness of pure and mixed pairs, the expected proportion of hybrids can be estimated from frequencies of matings: this should be equal to the proportion of heterospecific pairs among all pairs involving pure phenotypes. In the case of the mixed population studied here, the expected proportion of hybrids is 0.324 (bootstrapped 95% confidence intervals 0.251–0.403, $N = 139$ breeding pairs involving pure phenotypes; data from Zagalska-Neubauer & Neubauer, 2012). In turn, the observed proportions of hybrids, though variable depending on year, were always lower, reaching on average 0.211 (95% CIs: 0.181–0.243), indicating selection against hybrids.

The reproductive output of F_1 hybrids is usually used as a proxy for estimating fitness costs of hybridization. This is likely to lead to an underestimation, as fitness consequences could be severe in backcross generations descended from hybrid matings. Using highly informative single nucleotide polymorphism markers and data on reproductive success, Wiley *et al.* (2009) estimated multigeneration post-zygotic isolation between hybridizing flycatchers in Sweden. They showed that hybridization results in only 2.4–2.7% of the number of

descendants typical of conspecific pairing in second-generation backcrosses. Post-zygotic isolation thus appeared to be much more severe than previously thought and estimated using data on F_1 hybrids alone (Wiley *et al.*, 2009). Regrettably, it is impossible to obtain such a precise estimate in the present study, because backcrosses are indistinguishable from F_1 hybrids. With just one class of hybrids adopted, we were unable to follow fitness estimates over multiple generations in our hybrid zone, which limits our conclusions. Hence, we cannot rule out the possibility that, as in the flycatcher case, the fitness reduction in hybrids is actually greater than what we assessed based solely on the adult survival presented in this study. On the other hand, hybrids may not exhibit any intrinsic loss of fitness. For example, in one of the best studied cases of hybridization (despite not being from the classical secondary contact zone), interspecific hybrids between Darwin's finches (*Geospiza fortis* × *G. fuliginosa* and *G. fortis* × *G. scandens*) did not show any reduction in relative fitness: this was determined by an appropriate food supply (Grant & Grant, 1993). These hybrids were both viable and fertile (Grant & Grant, 2010; Grant *et al.*, 2004), survived just as well or better than the parental species, and had the same rate of mating and reproductive success (Grant & Grant, 1997a,b, 2010).

To summarize, along with the moderate assortative mating between herring and Caspian gulls documented in our earlier study, reduced adult survival represents the mechanism that reduces gene flow between these hybridizing gull species. The reported differences in adult survival and longevity between the hybrid gull females and their two parental species are of importance for the dynamics of the contact zone, by limiting the production of F_2 hybrids and backcross hybrid offspring. The fact that, on average, the reproductive (adult) phase of life is reduced by one quarter in female hybrids compared with females of parental species may contribute to the post-zygotic reproductive barrier and reduce gene flow. Given the current state of knowledge, we cannot conclude definitively that the lower survival of the heterogametic sex in avian hybrids commonly reduces the numbers of hybrids in the contact zones between hybridizing species; however, it is at least likely to contribute to it.

Acknowledgments

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