NOTE / NOTE

Natural hybridization between Dall's porpoises (*Phocoenoides dalli*) and harbour porpoises (*Phocoena phocoena*)

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Abstract: Natural hybridization occurs rarely in mammals compared with other taxonomic groups of animals. Cetaceans appear unique among mammals in exhibiting striking karyological uniformity, which suggests that they have the potential to produce hybrid offspring more readily than other mammals. However, the detection and accurate identification of wild mammalian hybrids is difficult, and molecular evidence for wild cetacean hybrids is extremely limited. Here, we present molecular and morphological evidence of frequent hybridization between free-ranging Dall's, *Phocoenoides dalli* (True, 1885), and harbour, *Phocoena phocoena* (L., 1758), porpoises. The study describes a temporally and geographically concentrated case of natural hybridization in large mammals. Molecular analyses of mitochondrial and nuclear DNA revealed the species identity, sex, and direction of cross of several hybrid individuals. In concert with morphological and behavioural observations, these data confirmed the hybrid status of putative crosses in the field, including reproductive females. All crosses examined had Dall's porpoise as the maternal parent. This directionality may reflect the indiscriminate pursuit of female porpoises by male harbour porpoises. Our finding of extensive localized hybridization, despite apparently strong isolation elsewhere in their range, suggests that ecological influences on mating behaviour may be of primary importance in the reproductive isolation of these, and possibly other, cetacean species.

Résumé : Il y a rarement de l'hybridation naturelle chez les mammifères, comparativement à d'autres groupes taxonomiques d'animaux. Les cétacés se distinguent parmi les mammifères par leur remarquable uniformité caryologique, ce qui laisse croire qu'ils ont le potentiel de produire des rejetons hybrides plus facilement que les autres mammifères. Cependant, la découverte et l'identification précise des hybrides chez les mammifères sauvages sont difficiles et il y a très peu de données moléculaires qui confirment l'existence d'hybrides chez les cétacés en nature. Nous présentons ici des données moléculaires et morphologiques qui appuient l'existence de croisements fréquents en nature entre le marsouin de Dall, *Phocoenoides dalli* (True, 1885), et le marsouin commun, *Phocoena phocoena* (L., 1758). Il s'agit d'une étude de cas circonscrite dans le temps et l'espace d'une hybridation naturelle chez de grands mammifères. Les analyses moléculaires de l'ADN mitochondrial et nucléaire ont permis d'identifier l'espèce, le sexe et le sens du croisement chez plusieurs individus hybrides. Combinées aux observations morphologiques et comportementales, ces données confirment le statut hybride de croisements putatifs en nature, ainsi que celui de femelles reproductives. Dans tous les croisements observés, le parent maternel est un marsouin de Dall. Ce phénomène s'explique peut-être par la poursuite sans distinction des marsouins femelles par les mâles du marsouin commun. Notre découverte d'une importante hybridation locale, malgré apparemment un fort isolement reproductif ailleurs dans la zone de répartition géographique,

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indique que les effets des facteurs écologiques sont d'importance capitale pour l'isolement reproductif chez ces espèces de cétacés et probablement aussi chez d'autres.

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Introduction

Natural hybridization occurs rarely in mammals (Gray 1971), although it can be widespread in other taxonomic groups (Hubbs 1955; Grant and Grant 1992; Arnold 1997). The uniquely rapid chromosomal evolution of mammals is thought responsible for their relative inability to hybridize (Wilson et al. 1974; Prager and Wilson 1975). Cetaceans (whales, dolphins, and porpoises) are unusual in displaying prominent karyological uniformity (Árnason 1972, 1982), suggesting that they may have the potential to produce viable hybrid offspring more easily than other mammals (Árnason et al. 1991). Although cases of hybridization between captive cetaceans support this hypothesis (e.g., Sylvestre and Tasaka 1985; Zornetzer and Duffield 2003), only a few cases have been suspected among wild cetaceans (see review by Bérubé 2002). Molecular evidence of wild cetacean hybrids has to date been limited to only five animals: four crosses between fin, *Balaenoptera physalus* (L., 1758), and blue, *Balaenoptera musculus* (L., 1758), whales (Árnason et al. 1991; Spilliaert et al. 1991; Bérubé and Aguilar 1998) and a Dall's porpoise × harbour porpoise, *Phocoenoides dalli* (True, 1885) × *Phocoena phocoena* (L., 1758), fetus (Baird et al. 1998). Identification of the morphologically distinctive porpoise fetus prompted speculation regarding the possible hybrid status of numerous uniquely pigmented porpoises in the waters surrounding lower Vancouver Island, British Columbia (Baird et al. 1998), which, if confirmed, would represent the most extensive known occurrence of natural cetacean hybridization and one of the most geographically concentrated cases of hybridization in large mammals.

Mitochondrial DNA (mtDNA) studies have been useful in documenting introgression in a few mammalian species pairs in the wild, confirming the occurrence of past hybridization events (e.g., mice, Ferris et al. 1983; deer, Carr et al. 1986; voles, Tegelström 1987; wolves/coyotes, Lehman et al. 1991). However, documentation of mammalian hybrids themselves occurs infrequently because of the challenges inherent in locating and accurately identifying them. Here, we investigate the hybrid status of putative hybrid porpoises through molecular analyses of mtDNA and nuclear DNA, in concert with morphological and behavioural observations at sea. We then address the directionality (maternal species vs. paternal species), fertility, and sex-dependent viability of hybrid crosses to provide insight into the potential causes and consequences of hybridization in these species.

Materials and methods

Study species and general methods

Dall's and harbour porpoises are morphologically and ecologically distinct species, sympatric in many coastal regions of the North Pacific (Gaskin et al. 1974; Jefferson 1988). The two species diverged sometime within the last 2–

3 million years (Rosel et al. 1995) and share the same chromosome number, $2n = 44$ (Kulu et al. 1971; Árnason 1974). Both species occur regularly in the waters between southern Vancouver Island, British Columbia, Canada, and the US San Juan Islands (Baird and Guenther 1994), particularly in the study area of Haro Strait (48°35′N, 123°16′W), but do not form mixed groups. Breeding is seasonal and overlapping between the species (Jefferson 1988; Gaskin 1992).

Boat-based data were collected within a <60-km^2 area of Haro Strait from June to early September 1997 and 1998 as part of a larger study of porpoise mating behaviour (Willis 2001). Putative hybrids were identified visually based on their distinctive external morphology, particularly their pale gray pigmentation (see Table 1), and photographed when possible. Skin tissue was biopsy-sampled from seven putative hybrids using either a crossbow or a pole spear equipped with custom-made sampling tips (W. Hoggard, Pascagoula, Mississippi, USA; CETA-DART, Virum, Denmark), with two additional putative hybrid tissue samples obtained via a concurrent study by Hanson (2001; M.B. Hanson, unpublished data) in the same region. Samples were stored in a sodium chloride – dimethyl sulfoxide solution. Additional samples were collected from archived tissues of locally stranded Dall's and harbour porpoises. All samples were frozen at –70 °C until analyzed. Field research was conducted in accordance with the principles and guidelines of the Canadian Council on Animal Care and approved by the Simon Fraser University Animal Care Committee (project No. 514B).

DNA extraction

Small pieces (1–2 mm^3) of skin tissue were macerated as finely as possible using razorblades and digested in 900 µL of Lifton buffer (0.2 mol sucrose/L, 0.05 mol EDTA/L, 0.1 mol Tris/L, 0.5% *w/v* SDS). The homogenate was extracted with ~100 µL of CHCl$_3$ and ~100–500 µL of phenol and then precipitated with 30 µL of 7.5 mol NH$_4$OAc/L and ~500 µL of isopropanol. DNA pellets were washed with 70% ethanol, dried overnight, resuspended in 50 µL of distilled deionized water, and stored at –20 °C.

Polymerase chain reactions (PCRs)

As mtDNA is maternally inherited, we identified the maternal parent of putative hybrids by amplifying and sequencing a 230 base pair (bp) portion of the mtDNA cytochrome *b* region that demonstrates species-level variation (Rosel et al. 1995). mtDNA amplification with primers designed from sequence data provided in Rosel et al. (1995) (CYTB-A 5′-CGT GGC CTA TAT TAC GGC TCC TA-3′ paired with CYTB-B 5′-GTT AGT GTT GCT TTG TCT ACG G-3′) was conducted in 25-µL volume reactions using ReddyMix^{TM} PCR Master Mix (ABgene, Surrey, UK) containing 0.75 unit of *Taq* DNA polymerase, 75 mmol Tris–HCl/L (pH 8.8 at 25 °C), 20 mmol (NH$_4$)$_2$SO$_4$/L, 1.5 mmol MgCl$_2$/L, 0.01% *v/v* Tween 20, and 0.2 mmol/L each of dATP, dCTP, dGTP,

Table 1. Morphological, behavioural, and genetic traits distinguishing Dall's (*Phocoenoides dalli*), harbour (*Phocoena phocoena*), and hybrid porpoises.

	Dall's	Harbour	Hybrid	Source(s)
Morphological				
Size and shape	Large, robust	Small, less robust	Intermediate	Jefferson 1990; Gaskin 1992; Baird et al. 1998; M.B. Hanson, unpublished data; P.M. Willis, personal observations
Dorsal fin size, shape	Tall, slightly falcate	Small, low, scalene	Intermediate	Jefferson 1990; Gaskin 1992; Baird et al. 1998; P.M. Willis, unpublished data
Dorsal fin pigmentation	Black with white frosting	Dark gray	Pale to dark gray, variable dark edge	Jefferson 1990; Gaskin 1992; P.M. Willis, unpublished data
Dorsal fin tubercles	Absent	Present	Present (always?)	Jefferson 1990; Gaskin 1992; M.B. Hanson, unpublished data
Body pigmentation	Black with white flank patch	Dark gray, pale ventrally	Pale to medium gray, variable dark gray to brown areas	Jefferson 1990; Gaskin 1992; Baird et al. 1998; P.M. Willis, unpublished data
Mouth-to-flipper stripe	Absent	Present	Present (always?)	Gaskin et al. 1974; Jefferson 1988; Baird et al. 1998; M.B. Hanson, unpublished data
No. of vertebrae	92–98	62–66	Approximately 75	Gaskin et al. 1974; Jefferson 1988; Baird et al. 1998
Behavioural				
Bowriding	Frequently	Never	Intermediate	Gaskin et al. 1974; Jefferson 1988; Baird et al. 1998; P.M. Willis, unpublished data
Typical surfacing	High, boxy	Low, smooth	Intermediate	Taylor and Dawson 1984; Jefferson 1988; P.M. Willis, personal observation
Rapid surfacing in "roostertail"	Yes	No	Yes	Taylor and Dawson 1984; Jefferson 1988; P.M. Willis, personal observation
Genetic				
Restriction fragment length polymorphism banding pattern affinity	(–) Harbour	(+) Harbour	(+) Harbour	Baird et al. 1998
mtDNA species affinity	Dall's	Harbour	Dall's	Rosel et al. 1995; present study
ZFX species affinity	Dall's	Harbour	Heterozygous	Present study
Intersimple sequence repeat banding pattern affinity	(–) Harbour	(+) Harbour	(+) Harbour	Present study

and dTTP. Reactions contained 10–200 µg extracted DNA/mL and approximately 100 ng of each primer. Thermal cycler parameters were 30 cycles of 60 s at 94 °C, 60 s at 47 °C, and 60 s at 72 °C.

The sex of odontocete cetaceans can be determined via amplification of a portion of the last exon in the *ZFX/ZFY* gene of the sex chromosomes (Bérubé and Palsbøll 1996). We followed the procedures outlined in Bérubé and Palsbøll (1996) using primers ZFYX0582F (5′-ATA GGT CTG CAG ACT CTT CTA-3′), ZFY0767R (5′-TTT GTG TGA ACT GAA ATT ACA-3′), and ZFX0923R (5′-AGA ATA TGG CGA CTT AGA ACG-3′). Amplification products were electrophoresed through 2% agarose gels stained with ethidium bromide and viewed under UV light.

To determine the paternal species of putative hybrids, we first used species-specific nuclear markers to identify parental DNAs in putative hybrids; these data were then considered in concert with the mtDNA data to infer the paternal species. Species markers were isolated through amplification of intersimple sequence repeats (ISSRs) and sequencing of *ZFX/Y* product (see below). ISSRs are short regions of nuclear DNA that lie between inversely oriented, simple sequence repeats (microsatellites), only recently used in the study of animal populations (Kostia et al. 2000). As spectrophotometer analysis revealed insufficient DNA in four putative hybrid extractions to carry out standardized ISSR amplifications, only five individuals were subjected to this analysis. Amplifications were conducted using primer 811 (5′-GAG AGA GAG AGA GAG AC-3′; University of British Columbia Nucleic Acid – Protein Service Unit, UBC Primer Set No. 9) in 20-µL reactions containing 0.035 µg of total DNA, 10× PCR buffer (200 mmol $(NH_4)_2SO_4$/L, 750 mmol Tris–HCl/L (pH 8.8), 0.2% *v/v* Tween 20 (TetraLink International, Amherst, New York, USA)),

0.25 mmol/L of each dNTP, 0.75 mmol/L of each primer, 3.1 mmol MgCl$_2$/L, and 0.25 unit of *Taq* DNA polymerase (UltraTherm^{TM}, TetraLink International). The cycling profile started at 94 °C for 1 min and 30 s for one cycle and then 94 °C for 30 s, 68 °C for 30 s, and 72 °C for 60 s for one cycle. The annealing temperature was reduced by 0.7 °C for each of an additional 12 cycles to help increase band specificity followed by 33 cycles as follows: 94 °C for 30s, 55 °C for 30 s, and 72 °C for 60 s. Reaction products were visualized under UV light on 1%–1.7% agarose gels stained with ethidium bromide.

Sequencing

Sequencing of mtDNA and *ZFX/Y* product for use in parental species determinations was conducted as follows. Amplified product for both strands was processed by adding 3–10 μL of product to 0.9 μL of each of exonuclease I (E.C. 3.1.11.1) and shrimp alkaline phosphatase (E.C. 3.1.3.1) and then cycled for 15 min at 37 °C and 15 min at 80 °C. Cleaned PCR products were sequenced using the BigDye^{TM} Terminator Cycle Sequencing Kit (Applied Biosystems, Foster City, California, USA). Electropherograms of sequence nucleotides were examined visually for sequence reliability and clarity. Heterozygosities were scored from both forward- and reverse-sequence electropherograms as superimposed peaks of approximately half intensity.

Results

We encountered putative hybrids on 79% of study days (117/148), typically as a single encounter but with as many as four different individuals observed in a day. They occurred most commonly in association with Dall's porpoises (130 sightings) and occasionally alone or with each other (21 sightings), but they were never observed with harbour porpoises. Variation between putative hybrids in the shade and patterning of body pigmentation, and in other traits such as body size and dorsal fin shape, permitted the individual recognition and photo-identification of several animals, and we estimate that a minimum of 20 putative hybrid individuals frequented the study area. No putative hybrids were observed exhibiting the striking secondary sexual characteristics of adult male Dall's porpoises (Jefferson 1990), suggesting either that male putative hybrids resemble male harbour porpoises in the absence of such characters at sexual maturity (Fontaine and Barrette 1997) or that male putative hybrids, while viable (see below), do not attain sexual maturity. Putative hybrid females were at least sometimes fertile, as we documented two different individuals with neonatal calves.

Variation in morphology, sequence data, and ISSR and *ZFX/Y* banding patterns demonstrated that no individual was biopsy-sampled more than once. mtDNA sequencing revealed a 6.5% divergence between Dall's and harbour porpoise sequences. We found complete concordance of sequences from all nine putative hybrids with those of Dall's porpoises at the 11 sites differentiating species; these data identify Dall's porpoise exclusively as the maternal parent species (Fig. 1) (GenBank accession Nos. AY222440–AY222454). Visualization of ISSR amplification products revealed both individual and species variation in banding

Fig. 1. Polymorphic positions (relative to the reference sequence Pdal1) of Dall's (*Phocoenoides dalli*), hybrid, and harbour (*Phocoena phocoena*) porpoise cytochrome *b* sequences. A full stop indicates conformity with the Pdal1 sequence. Dashes indicate nonsequenced sites. See GenBank for full sequences. *Reference sequence data from Rosel et al. (1995) are included for comparison; †a Black Sea (allopatric) specimen.

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                2 2 3 3 3 3 3 3 3 3 3 3 3 4 4 4 4 4 4 4 4 4 4 4
                8 8 0 1 1 1 1 2 4 5 6 8 0 1 2 2 2 3 3 3 4 4 6
                4 7 5 1 4 7 8 0 1 3 8 0 1 1 1 5 8 1 6 7 0 9 1

       Pdal1*   T A T T A T C T C C G A T C T T C T A T A G G
       Pdal2*   . . . . . . . . T . . . . . . . . . . . . . .
Dall's DP9705   . . . . . . . . . . . . T . . . . . . . . . .
       DP0619   . . . . . . . . . . . A . . . . . . . . . . .
       DP9710   - - . . . . . . . . . . T . . . . . . . . . .
       DP9716   - - . . . . . . . . . . . . . . . . . . . . .
       Y82897   . . . . . . . . . . . . T . . . . . . . . . .
       Y52597   . . . . . . . . . . . . . . . . . . . . . . .
       Y61397   . . . . . . . . C . . C . . . . . . . . . . .
hybrid Y9804    . . . . . . . . . . . . . . . . . . . . . . .
       Y9801    . . . . . . . . . . . . T . . . . . . . . . .
       Y9803    . . . . . . . . . . . . T . . . . . . . . . .
       Y9805    . . . . . . . . . . . . . . . . . . . . . . .
       Y628     . . . . . . . . . . . . T . . . . . . . . . .
       Y61698   - - - - . . . . . . . . . . . . . . . . . . .
       HP9513   - - - G G C T A . . A . C . . C T C G C G . .
harbour HP9518  C G . G G C T A . . A . C . . C T C G C G . .
       Ppho1*   C G . G G C T A . . A . C . . C T C G C G . .
       Ppho2*   C G . G G C T A . . A . C . . C T C G C G . .
       PpBS*†   C . C G G C T A . T A . C . . C T C G C . A A
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Fig. 2. Intersimple sequence repeat fragments generated by polymerase chain reactions from harbour (lanes 2–5), hybrid (lanes 6–9), and Dall's porpoises (lanes 10–15); 100-bp ladders in lanes 1 and 16. The slight variation in ~670-bp fragment positions may reflect variation in the number of microsatellite repeats.
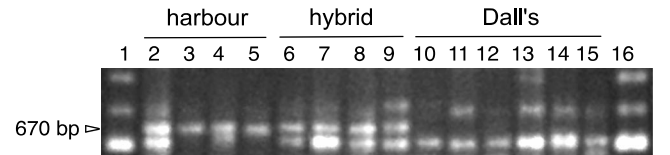
patterns (Fig. 2). As only species-specific bands were informative in hybrid identification, only these were considered. A ~670-bp band specific to harbour porpoises, but absent in Dall's porpoises, also appeared in all five putative hybrids analyzed (Fig. 2). These results were consistent over several runs. As the maternal species of putative hybrids was identified as Dall's porpoise, the origin of the harbour porpoise specific band must be paternal, identifying suspect porpoises as hybrids.

ZFX/Y amplification products revealed a 5:4 male to female sex ratio of sampled putative hybrids. Sequencing of *ZFY* (male) product revealed no between-species variation (GenBank accession Nos. AY257193–AY257196). However, one site (position 103) within the six *ZFX* sequences from Dall's and harbour porpoise females differed between the two species, with all four female putative hybrids (including one not subjected to ISSR analysis) scoring as heterozygous (GenBank accession Nos. AY257183–AY257192). The frequency of heterozygous individuals is significantly different between the putative hybrids (four of four) and parents (one of six) (Fisher's exact test, $p = 0.0476$). A qualitatively simi-

lar pattern appears at a second site (position 178) where two putative hybrids and one Dall's porpoise appear as heterozygotes (Genbank accession Nos. AY257183–AY257192). These sequence data further support a hybrid classification.

Behavioural and morphological characters intermediate between harbour and Dall's porpoises or common to only one parental species have been noted for putative hybrids in the wild and documented for the hybrid fetus described previously (Baird et al. 1998) (Table 1). From these data, our observations at sea, and the results described above, we summarize the available morphological, behavioural, and molecular evidence differentiating the porpoise types and identifying hybrids in Table 1.

Discussion

This study provides strong evidence of recurrent hybridization between local populations of Dall's and harbour porpoises and is one of only a few studies identifying mammalian hybrids in the wild, including their sex and direction of descent. Our findings support the hypothesis that the slow chromosomal evolution of cetaceans enables them to produce hybrid offspring more easily than other mammalian taxa (Árnason et al. 1991). The 6.5% cytochrome b mtDNA divergence reported here between harbour and Dall's porpoises approaches that observed between blue and fin whales (7.6%; Árnason and Gullberg 1993), the latter species pair being among the most distantly related mammalian species pair known to hybridize (Árnason et al. 1991; Árnason and Gullberg 1993). It appears that cetacean hybridization in the wild is possible even despite substantial mtDNA divergence and long separation times. However, the porpoises studied here are only the second cetacean species pair for which strong evidence of recurring natural hybridization is available and the first for which the production of viable offspring by female hybrids in the wild has been documented. If cetaceans as a group indeed face fewer postzygotic barriers to hybridization than other mammals, then pre-zygotic factors likely play a prominent role in reproductively isolating member species, as has been suggested for blue and fin whales (Spilliaert et al. 1991).

The evolutionary consequences of porpoise hybridization are difficult to predict without measures of hybrid fertility and viability, which are beyond the scope of the present study. However, female hybrids are at least sometimes fertile, as evidenced through observations of hybrid females with neonatal calves. The presence of a fetus in a female blue × fin whale hybrid suggests some fertility in these crosses as well (Spilliaert et al. 1991; Árnason and Gullberg 1993). Similarity between species karyotypes likely reduces meiotic incompatibly in female blue × fin whale hybrids (Árnason and Gullberg 1993) and may operate similarly in porpoises. Although the 5:4 male:female sex ratio of sampled hybrids suggests equal viability between the sexes, the predominance of male sterility in other mammalian crosses (Gray 1971; Wu et al. 1996) and the observation of probable sterility in another male cetacean hybrid (blue × fin whale; Árnason et al. 1991) suggest that male porpoise hybrids may be infertile. Porpoise hybrids may therefore be expected to exhibit reduced average fertility with respect to parentals, which should select against hybridization. However, the presence of F_2s suggests that introgression may be occurring, presumably via female hybrids back-crossing to one or both parental species.

Examples of multiple hybridization events among large mammals in the wild are few (e.g., Carr et al. 1986; Lehman et al. 1991; Goldsworthy et al. 1999). The porpoise hybrids reported here represent a temporally and geographically concentrated case of natural hybridization in large mammals. Although we believe incidental descriptions of white or gray "Dall's" porpoises from other regions of sympatry to be misidentified hybrids (e.g., Morejohn et al. 1973; Joyce et al. 1982; Miller 1990), the present study region appears unique in hosting many hybrids over a very small area, only a small fraction of the parental species' range of sympatry. Why this localized hybridization should be occurring despite apparently strong isolation elsewhere is unclear, but it may reflect the apparent decline in local harbour porpoise numbers over the last several decades (Baird 2003). Natural hybridization events among other mammalian species almost always involve disturbed habitats where one population is in decline (e.g., Carr et al. 1986; Lehman et al. 1991). A decrease in the availability of conspecific potential mates may increase the cost of choice to individuals, so that some populations, otherwise acting as "good species", begin hybridizing (Wilson and Hedrick 1982). Harbour porpoise males may be pursuing matings indiscriminately, including matings with heterospecifics, partly in response to a lower conspecific encounter rate.

All analyzed hybrids had Dall's porpoises as maternal parents, as did the hybrid fetus reported previously (Baird et al. 1998). This directionality is among the strongest observed in hybridizing animal populations and it contradicts the recent prediction that in species displaying female choice, females of the rarer species should act as the maternal parent (Wirtz 1999). We suggest that the highly promiscuous male harbour porpoise (Fontaine and Barrette 1997) may be driving hybridization in the observed direction through the indiscriminate pursuit of females of either species. Indiscriminate and forceful or "sneaky" male mating behaviour may be common to animal hybridization events, including those occurring directionally (e.g., Lamb and Avise 1986; Spence 1990), particularly if males are of the rarer species (e.g., Goldsworthy et al. 1999). Further study of premating isolation in hybridizing animal species is needed to test these predictions.

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