**General comments**

We offer responses specific to various reviewer comments later in this reply to reviews. But we begin with two observations that seem to underlie differences between us and the reviewers and that make us unwilling to greatly modify the manuscript, even though a major revision and shortening has been requested by one of the reviewers.

First, neither reviewer mentions the fundamental point of this paper, namely, that we are seeking the beginnings of an answer to the question of why hybrids vary so much in frequency between broadly sympatric species. This is the issue we are trying to develop, and the case study of albatrosses is simply meant to demonstrate how we can use predictions of siring asymmetries to test the idea that relatively high frequencies of hybrids may, in some groups, be caused by heterospecific rape. Following the “They say, I say” Paradigm of scientific writing (Graff and Berkenstein 2009), we opened this paper with reference to the Wirtz (1999) review of asymmetric hybridization because we are using siring asymmetries to test predictions of our hypothesis of heterospecific rape. (We also note that these asymmetries apply to some cases of heterospecific brood parasitism but not to others.) The fundamental point here is not that hybridization is asymmetrical, but that we are using the behavior and the biology of the parental species to predict the *direction* of the asymmetry, that is, to predict the siring species. We have revised the opening paragraph to try to make these general points clearer, also adding reference to the review by Grant and Grant (1992) of variations in the frequency of hybrids across different avian groups.

The second observation relates to our small sample of six hybrid albatrosses. Certainly more hybrids would be desirable, but the siring asymmetry we observed was predicted before these samples were analyzed, based on an extensive knowledge of the literature on these albatrosses that S. Rohwer had studied for other projects on their life histories. Fisher’s (1971) graphic descriptions of conspecific rapes in Laysan Albatrosses made it difficult not to be interested in rape as the origin of these hybrids, even if he did not think they were the product of forced copulations. We tried and failed to find additional blood or tissue samples, and we do not have the funds or facilities for analyzing DNA amplified from museum specimens. If we take the Fisher’s exact probability seriously, another sample of F1 hybrids should also show a siring bias. More importantly, our thesis that heterospecific rape is an important source of hybrids in broadly sympatric species with forced copulations, can only be generalized by tests with other appropriate species pairs. Of course a larger sample would inspire more confidence in this single case study, but that would have little affect on our confidence in the general thesis we espouse. (To this end, one of us is assembling a sample of hybrid ducks, though that is irrelevant to these reviews.)

Given that we cannot test the hypothesis of heterospecific rape generally, it is fair to ask if these results for albatrosses should be published as the case study we develop. We think so for two reasons. First, this is a reasonable package size, and there are few other relevant studies, other than the swallow observations we review. Second, given the weakness of Randler’s (2005) comparative tests, developing these stronger predictions for testing heterospecific rape (and brood parasitism) may stimulate further tests.

In general we think the revisions we have made address the spirit of the reviewer’s comments. We have added more detail from Fisher’s description of forced copulations, clarified information in the tables, and added more information on the molecular methods. We have also expanded the first and last paragraphs to make clear that this case study is intended to show how the hypothesis of heterospecific rape might be tested with greater strength, and to make clear that we do not presume our results offer a general evaluation for the idea; a general evaluation can come only from studies of other appropriate hybridizing species pairs.

**Response to Reviewer 1 (Patricia Brennan)**

**There is no description presented on how these forced copulations take place….**

We agree, and have added a good bit more detail that we omitted because of normal space limitations. The rapes are violent, sometimes resulting in severe female injury and often involving many males. Surprisingly, Fisher does not report observations of the female’s mate defending her, as occurs in waterfowl. If an everted cloaca is essential for a female receiving sperm, then the extreme aggression of these rapes, which may result in females being blinded, suggest acquiescence to the harassment, as Brennan implies.

**It is true that there is heterospecific rape in ducks, however, ducks often form heterospecific pair bonds as a result of brood parasitism….**

Again, in the interest of brevity we cut discussion of heterospecific parasitism from this version of the manuscript. Now we have added some of that back to this version. In some cases these hypotheses can be distinguished by predicting siring asymmetries. For example, Redheads parasitize Canvasbacks, but not vice versa, so hybrids (which are relatively common) between this species pair should have Canvasback sires. In contrast Barrows and Common Goldeneyes are reciprocal parasites, so no siring asymmetry is predicted between their hybrids, which are also relatively common.

**For the reason stated above, I think that unidirectional pair bonds would also have the same results.**

The problem we see with this argument is that, if generalized to many females, it should result in the complete breakdown of species boundaries, yet this is not what we see. Rather, heterospecific pair bounds seem to be rare. Even in the case of Mallards and Black Ducks, where Mallards are dominant and have an advantage over Black Ducks in competition for unmated Black Duck females (Brodsky et al. 1988), most hybrids seem to result renesting females that are harassed by more aggressive male mallards freed of mate guarding because their females are on eggs. Thus, hybrids are more common where mallards are relatively more common (because there are more mallard males to harass renesting female Black Ducks), and hybrids are also more common where Black Ducks are relatively more common (because there are more renesting female Black Ducks to be harassed by male Mallards (Ankney et al. 1987).

**I disagree. Randler 2005 tested this hypothesis in waterfowl quite extensively (though perhaps not using the best approach).**

We agree, and have tempered this statement accordingly. We definitely do not wish to benign Randler’s great effort to do important comparative tests.

**Response to Reviewer 2 (Jennifer Walsh)**

**The background literature review could be better developed…..**

Jennifer is right that Fisher (1972) considered forced copulations a possible source of hybrids, but dismissed them because he saw none occurring between species. In the interest of text economy, we chose to ignore this statement and to cite instead McKee and Pyle (2002), who report interspecific rapes attempts, all of which (number not specified) were male Blackfoots harassing female Laysans. Their paper is more recent and their observations were made after the importance of forced copulations in waterfowl was well established (Barash 1977).

Hopefully the material we have added in the introduction will suffice to further develop the reasons we are emphasizing the importance of predicting siring asymmetries to study rape as a cause of unidirectional hybridization. As we note above, female choice, if at all general to a species, should quickly result in the breakdown of species boundaries, yet this does not appear to be occurring in waterfowl with broadly sympatric breeding ranges.

**Line 70 mentions the use of molecular methods to assess backcrossed individuals. A reference to this work or a summary would help clarify the context of the current research.**

A reference is scarcely needed for the simple calculations we do in Table 2.

**My biggest concern with the paper is that the data collected do not actually test the predictions made by the authors.**

Here the reviewer seems to be asking the impossible, namely that we observe a heterospecific rape, follow the egg and hatchling for the three or more years required for it to return to the breeding colony in adult breeding plumage, find it to be of hybrid phenotype, and finally determine that it was actually sired by the male that raped the female. Of course Jennifer Walsh is trying to make the point that there are alternate explanations for unidirectional hybridization, and that “the data do not speak directly to any of those mechanisms.” But the general point of this paper is not this case study of albatrosses. Rather, it is to use this species pair, whose reproductive behavior, has been very well described to generate a case study of how the biology and behavior of a species pair could be used to predict the sire of F1 hybrids under a hypothesis of heterospecific rape. If those predictions turn out to be confirmed for other species pairs, particularly in waterfowl and grouse, then the hypothesis would seem to be useful. Of course we will not be able to prove the mechanism through these predictions, but that is precisely the more general point: We develop theory and make predictions to understand things about the world that we cannot see directly.

McKee and Pyle (2002) had been cited for reporting interspecific forced copulations; we have made that observation even more explicit in this revision.

**Throughout, replace the word “rape” with “forced copulation”. Rape is rarely used in current animal behavior literature.**

It is true that rape is seldom used in the Animal Behavior literature, mostly because earlier social scientists interpreted rape in humans as something other than an alternate male reproductive tactic. That is no longer tenable so we prefer to call a spade a spade (see Thornhill’s work). “Heterospecific forced extrapair copulation” is quite the mouthful compared to “heterospecific rape”.

**Tables.**

We have revised the tables to make them easier to follow by a) adding a column to Table 1 that identifies the frequency difference between the parentals for the diagnostic loci, b) eliminating much of the complexity of Table 2, and c) describing the IM models in words in Table 3. Table 2 has been greatly simplified by presenting in Table 1 the dSNP frequencies needed to calculate the probabilities of finding the observed hybrid genotype in either F1 or backcross hybrids.

**IM, asymmetrical gene flow, and sample size.**

We are confused by Jennifer’s qualms with our sample size. The IM analysis was conducted with 29 and 28 individuals of the parental species and with 10 loci. This is equivalent to sample sizes used in other recent studies implementing IM (examples: Campagna et al. 2012 and Pavolva et al. 2013).

Yes, we recover overlapping confidence intervals for our estimates of gene flow. However, it is erroneous to determine the significance of the difference between two statistics based on overlapping confidence intervals. This is why we use L-mode in IM to choose the highest-ranking models. Our results show that models with unidirectional gene flow are consistently ranked the highest.

**Although informative, the sample size for putative hybrids is low. Choosing 6 putative hybrids based on plumage characteristics (which are reported to be highly variable in these species) limits the conclusions that can be made.**

We don’t understand this comment. Hybrids are too rare to be sampled other than by appearance, but this should in no way affect who was their sire.

**Based on the description of the population sampled, it appears that the unidirectional hybridization could still be based on a numbers game.**

This point is interesting, but implausible, and breaks the rule of “They say, I say” in science writing (which may be a little unfair on our part, but worth noting…!).

First, the reviewer’s point is exactly the opposite the most general explanation for asymmetric hybridization from the Wirtz’s (1999) review, namely that females facing extreme shortages of conspecific males pair with males of a more common relative. Jennifer’s suggestion would be somewhat plausible if Black-footed albatrosses were so rare that males could not find mates, but they number in the thousands on Midway, and the evidence is that young, unpaired males spend all their time courting females and are never involved in forced copulations. While the reviewer is turning this idea on its head, the point could apply in species where some males only engage in FEPC. However, Fisher’s observations suggest that female harassment in these albatrosses is always by mated males. Further, male Blackfoots (like female Blackfoots!) number in the thousands and have no shortage of mating opportunities, and courtship by unmated individuals generally occurs out of the breeding colonies. The unpaired hybrids observed by Fisher spent all their time courting females, despite being older than most unmated individuals.

**In general, the results do not strongly support the conclusions reached.**

We agree that “6 F1 hybrids with intermediate plumage from one location limits the conclusions that can be made system-wide.” But the point of this paper is not to prove this point beyond doubt for these albatrosses; rather, the point is to use these albatrosses as a case that illustrates how to generate stronger tests of the heterospecific rape hypothesis. Predictions similar to the ones we develop using the behavior and breeding biology of this species pair of to predict siring asymmetries must be developed and tested across a number species characterized by high frequencies of hybrids over broad areas of sympatry before we will know whether heterospecific rape can be regarded as a general explanation for the high frequency of hybrids between species pairs wherein at least one of the pair is characterized by conspecific rape.