A certain songbird exists in two types, Coastal and Inland, separated by a desert. The Inland form differs from the Coastal form by several chromosome rearrangements. As a result, if we bring birds from the two populations together, they are willing and able to mate, and have healthy young ("F1 generation"), but the young are completely sterile. They cannot assort their chromosomes correctly in meiosis to produce viable eggs or sperm. No grandchildren ("F2 generation") are produced.

Farmers irrigate the desert and birds can now cross it. If they mate with the wrong type, they will conduct courtship, build a nest, lay eggs, incubate the eggs and feed the young, but it's all useless as the offspring are sterile. During each step of this process the birds are at increased risk from predators due to distraction.

These birds live for several years and can produce a clutch of eggs each year.

1. (2 pts) Here are some *new genetic traits which could arise* in these birds. Number them in order of their usefulness in improving the fitness of the songbirds, with 1 being best and 5 being worst:

   - Hybrid young (F1) die shortly after hatching *(4)*
   - Purebred Coastal birds breed in a different season than Inland birds, and will not even try to court in the wrong season *(1)*
   - Hybrid eggs (F1) abort before they are laid *(3)*
   - Hybrid birds (F1) have unattractive plumage and cannot attract mates *(5)*
   - Purebred (Coastal or Inland) males will attempt to court foreign females, bringing them gifts and singing to them, but the females always reject them *(2)*

2. (5 pts) Briefly explain the reasoning you used in (1). *The earlier cross-species matings fail, the less time, energy and risk are involved. Separate breeding seasons are nearly no-cost (the only problem is that the new season might have worse weather than the original one). Courtship failure wastes some of the males' time. Aborting eggs probably wastes both parents' whole breeding season; dying hatchlings also waste the nesting period. Unattractive young are the most costly.*

3. (3 pts) Are there any traits on the list which could not be selected for at all? If so, which ones, and why? If all could be selected for, briefly explain how.

   The two pre-mating forms of isolation can be selected for directly: a bird which mates a bit earlier or later and thus avoids cross-species mating will have more fertile offspring on average. The egg-aborting and hatchling-death isolation can't be selected for directly, as that would be trying to select for a specific phenotype in an animal that can't reproduce anyway. But they could be selected by kin selection: for example, early abortion of useless hybrid eggs could improve survival of their non-hybrid half brothers and sisters, and that trait could therefore increase. It is hard, though, to see how ugly hybrids could be selected for. They would improve the fitness of the whole species, but that's not enough–for the allele to increase it must improve its own fitness either directly or indirectly. Birds could easily evolve the trait of finding the hybrids ugly, but the ugliness itself is hard to select for. Maybe kin selection if the birds stay in family groups; otherwise it would have to be group selection, which seldom works.

4. (3 pts) Some climatologists argue that the desert has been continuously present for thousands of years; others argue that during wetter decades it is fertile enough for songbirds to cross, and such wet decades occur frequently. Which theory do our songbirds support? Why?

   Continuous desert. If the birds often met they should have evolved some pre-mating isolation by now, but they haven't. I gave partial credit to answers that said the desert was continuous because otherwise speciation couldn't have happened at all, but this isn't necessarily true; you can have speciation with gene flow if there is strong selection for different adaptations.

5. (3 pts) We find several other species of songbirds closely related to the Coastal and Inland birds. All of them have the same chromosome arrangement as Coastal, whereas Inland has a unique chromosome arrangement. What does this suggest about the history of the Inland population?

Most likely Inland was a small isolated population which could fix chromosome rearrangements by drift. Many students said that this shows Inland was the most recent speciation, but I don't see the reasoning for this. If anything, species separated by multiple rearrangements might have separated longer ago than species which still have the same chromosomes.

6. (4 pts) Given all available evidence, including the chromosome data, what type or types of speciation events likely produced the Inland songbird species–parapatric, peripatric, allopatric, or sympatric? Why? (More than one answer may be reasonable.)

   Peripatric is most likely. The multiple chromosome rearrangments point strongly at a very small Inland population at some point in its history. Allopatric is the next best choice–it doesn't explain the rearrangements, but otherwise fits the evidence, and possibly the bottleneck that allowed the chromosome rearrangements to fix came after speciation. Parapatric or sympatric speciation are very unlikely as if there had been gene flow we would strongly expect pre-mating isolation to have evolved, and it has not (birds are "willing and able" to mate).