Biodiversity is the outcome of the processes of species formation and extinction. Species formation (speciation) is by far the lesser understood of those two processes, but it is clear that the heart of speciation is the evolution of reproductive isolation, that is, the failure of genes to move freely between two species (Mayr 1963, Harrison 1998). When genes do not move freely, each species is an independent evolutionary unit. In animals, the evolution of reproductive isolation is usually gradual, in contrast to plants, in which reproductive isolation can arise in only one generation through polyploidy, the multiplication of sets of chromosomes. Reproductive isolation can involve factors that affect either the probability of zygote formation (prezygotic isolation) or the viability or reproductive success of hybrids (postzygotic isolation). In this article, I focus on the former, exploring approaches to studying the evolution of prezygotic reproductive isolation in animals.

Reproductive isolation can evolve as a byproduct of ecological divergence or as a response to direct selection on reproduction (for a review of these topics, see Schluter 1998). Ecological divergence is the process of adaptation of different populations to different environments. Either pre- or postzygotic reproductive isolation may follow this divergence. Populations may not exchange genes because they have adapted to different niches, or populations in new environments may persist long enough for reproductive isolation to evolve because of the gradual accumulation of genetic differences, regardless of adaptation. Direct selection on reproduction—which can involve anything from long-distance attraction to courtship behavior to sperm-egg interactions (West-Eberhard 1983, Palumbi 1998)—generally produces prezygotic isolation.

As a factor in reproductive isolation, ecological divergence has received far more attention than behavioral and sperm-egg isolation, perhaps because until recently scientists focused more on how species maintain their distinctness than on how species form (Foster et al. 1998). Moreover, ecological divergence can be studied well by examining species that have already reached substantial reproductive isolation, whereas the question of how species form requires a study of populations that are in the process of diverging.

Darwin realized that oceanic islands are particularly valuable for the study of speciation. The waifs that manage to reach isolated archipelagoes and find a favorable habitat are in a situation that permits, and may promote, species formation. The Galapagos and Hawaiian islands thus are excellent sites for studies of speciation (Wagner and Funk 1995, Grant and Grant 1996), although other archipelagoes also are important (Clarke and Grant 1996). Of the many groups of plants and animals whose radiation has been studied in Hawaii, the Drosophila in particular, because of their diversity and elaborate mating displays (Ringo 1977), have stimulated research on the hypothesis that mating behavior can drive the process of speciation (Kaneshiro 1976).

Sexual selection and speciation

Sexual selection is that part of mating behavior that concerns mating success (Darwin 1871); it drives the evolution of extravagant male ornaments such as plumage, calls, pheromones, and antlers. These ornaments are usually disadvantageous to a male’s viability or survival, but they are advantageous in that they increase a male’s mating success. In most species, males have a high variance in mating success and thus are the sexually selected sex, whereas females have a uniformly high probability of mating and are rarely sexually selected. Sexual selection can involve both intersexual competition for access to mates and female choice among potential mates; the relative importance of these two processes differs among species.

Formal genetic models demonstrate that sexual selection can lead to speciation whether or not ecological divergence
is present. In a quantitative genetic model of an idea developed by Fisher (1958), Lande (1981) showed that even in the absence of ecological divergence, female mating preferences can alter male displays to such a point that the population can be considered a new species. This model assumes that both female preferences and male displays are controlled by several genes. Females are most likely to mate with males that they prefer; thus, their daughters will show a preference similar to their own and their sons will have a display similar to the father’s. Additionally—and critically—daughters carry the genes for the father’s display type and sons carry the genes for the mother’s preference (i.e., there is a genetic correlation between the preference and the trait). Because the preferences and the traits are correlated, a self-reinforcing genetic system is set up and the population can “run away” to mating behavior that is very different from the starting point. The endpoint can be so different that behavioral isolation, and thus a new species, evolves.

Although Lande’s original runaway model did not address ecological factors (Lande 1981), Lande and Kirkpatrick later modified the model to show that ecological divergence between populations can be accompanied by divergence in female mating preferences (Lande and Kirkpatrick 1988). Perhaps the most surprising results come from a later model generated by Turner and Burrows (1995), which also is based on the runaway process. These researchers showed that sympatric speciation (speciation with no geographic barrier to gene exchange) can be driven by female mating preferences. They found that if females are sufficiently choosy, sampling many males before accepting a mate, selection can be strong enough to prevent gene exchange between sympatric populations with differing types of displays. Before this model was presented, the process of sympatric speciation had been thought to be rare at best (Futuyma and May 1980). The recent model suggests, however, that sympatric speciation is far more plausible than many researchers had imagined.

Scientists have also used nonmathematical arguments to relate sexual selection to speciation. For example, Ringo (1977) proposed that the concomitant evolution of a new male display and female preference could result in reproductive isolation, which could explain the great diversity of secondary sexual characters among species of Hawaiian Drosophila. As a result of a study of four species of Hawaiian picture-winged Drosophila, another researcher, Kane-shiro (1976, 1980), developed the hypothesis that speciation in this group has been driven by sexual selection; he proposed that females in more derived populations would be less discriminating in their choice of males than females in ancestral populations because, in a small population after a founder event, females that were highly discriminating might not mate. West-Eberhard (1983) presented detailed arguments in support of the hypothesis that differences between animal species in mating behavior could be attributed to sexual selection. Her reasoning included the points that sexual selection is often both strong and directional and that the runaway process could be initiated by many genetic, behavioral, and ecological factors. She proposed that sexual selection could have driven speciation in many animal groups, including birds, insects, crabs, and lizards.

Both the genetic models and the verbal models propose that female mating preferences can change the mating behavior of a population so greatly that reproductive isolation can evolve. This proposition suggests a hypothesis for experimentation—namely, that sexual selection and speciation form a continuum, or, in other words, both sexual selection and behavioral isolation incorporate the same behavioral processes. This hypothesis was not included in the early ideas about the role of behavioral isolation in speciation (Dobzhansky 1970), and it has been denied by at least one influential evolutionary biologist (Paterson 1989), who argued that within a species, mate choice selects for the mean phenotype rather than an extreme phenotype. Previous studies of behavioral isolation between species suggest that the factors that cause isolation evolved from sexually selected characters (e.g., Ringo 1977, Phelan and Baker 1987, Ryan and Rand 1993).

One way to test whether sexual selection forms a continuum with behavioral isolation is to determine whether females are capable of responding to a heterospecific signal but nevertheless prefer a conspecific signal. This test was developed and illustrated by Ryan and Rand (1993), who showed that although female Physalaemus frogs would approach a playback of a heterospecific male call when it was paired with white noise in a two-speaker test, they preferred the call of a conspecific when it was paired with the heterospecific call. Another approach is to reason that, if the models demonstrating that sexual selection can drive speciation are valid, it should be possible to identify one or more sexually selected traits within one species (or population) that are involved also in the failure of attempts to cross the population with a close relative (Boake et al. 1997). This second approach guides my attempts to understand the role..
of sexual selection in speciation in the Hawaiian Drosophila.

The ideal animal groups for studies of sexual selection and speciation would be in the process of diverging so that differences between them, rather than evolving after gene flow had disappeared, might contribute to divergence. Furthermore, their mating behavior would emphasize male displays rather than a male’s ability to provide parental care or to present a high-quality territory to prospective mates. Such species would simplify the study by allowing the researcher to focus on mating displays. Another important feature that would enable a focus on mating behavior is minimal ecological divergence between the two groups being studied. The list of desiderata also includes the animal’s amenability to experimentation and the feasibility of laboratory rearing. The fly species described in this article meet many of these criteria: They are close relatives and the probability that their divergence was driven by sexual selection is high, as described in the next section.

Hawaii and its Drosophila
The remoteness and geological history of the Hawaiian islands make them an ideal location for studying evolution (Carson and Clague 1995). The islands formed over a hot spot in the earth’s crust. The youngest one, Hawaii, is approximately 400,000 years old; it has active volcanoes because it is close to the hot spot. The Pacific plate carries the islands to the northwest, and each island in that direction is successively older; Kauai, the oldest high island (one with mountains), is approximately 6 million years old. The atolls and seamounts to the northwest of Kauai are the remnants of former high islands. New islands have become available for colonization at intervals of approximately 1 million years. The original colonists of the archipelago may have come directly from a continent, but many colonizations have been from older islands within the chain (Wagner and Funk 1995). In some lineages, the ancestor may have arrived before the present high islands were formed.

The biogeography of Hawaii shows two different patterns of radiation (Wagner and Funk 1995). In some lineages, such as crickets in the genus Laupala, colonization of each island has resulted in adaptive radiation on the island; new species have formed to fill a variety of niches (Shaw 1995). In other lineages, such as the subgroup of Drosophila that I study, speciation is not accompanied by adaptive radiation—that is, the nearest relative of a particular species is most likely to be found on an adjacent island in the same kind of habitat and using the same kind of host plant (Kambyseulis and Heed 1971, Kaneshiro and Boake 1987, DeSalle 1995). Researchers postulate that each new Hawaiian Drosophila species formed as a result of a single insecminated female being blown in a storm to a previously unoccupied island (Kaneshiro 1976, Spieth 1981, Carson 1982).

The majority of research on speciation in Hawaiian Drosophila has been conducted with the large, picture-winged flies (Figure 1), particularly those in the planitibia subgroup. Four species, Drosophila heteroneura, Drosophila planitibia, Drosophila silvestris, and Drosophila heteroneura, are of particular interest. Each species is endemic to a single island in the chain (Figure 2), but all four species are similar in their ecology, occupying the same altitudes in cloud forest on each island. In all of the species, feeding and oviposition take place on rotting stems of plants in the genus Clermontia (Kambysellis and Heed 1971, Carson 1982, Carson et al. 1989). Males perch on the bare parts of tree fern fronds and defend territories that are 40–50 cm long against other males; females visit and mate with males at these perches (Spieth 1978). Some pairs are unlikely to hybridize in the laboratory for behavioral reasons (e.g., D. silvestris and D. heteroneura; Kaneshiro 1976); in other pairs, hybrid males that do result from laboratory mating are sterile (e.g., D. silvestris and D. planitibia; Craddock 1974). That their divergence is more behavioral than ecological makes these species excellent for the study of the role of mating behavior in speciation. Furthermore, because the four species represent various levels of genetic and behavioral divergence (DeSalle and Giddings 1986), they can be viewed as cross sections of the process of speciation.

Introduction to D. silvestris and D. heteroneura
The species D. silvestris and D. heteroneura are sympatric on the island of Hawaii (Figure 2). Based on genetic data, they appear to be the most closely related pair of species in the planitibia subgroup. Both species have chromosomal inversions that differ from those in most other Hawaiian Drosophila, but all the inversions are found in both species.

Figure 2. Hawaiian island chain with the locations of the four youngest species in the planitibia subgroup. Drosophila planitibia is thought to be ancestral to the other three species, with Drosophila heteroneura most likely having arisen from Drosophila silvestris (DeSalle and Giddings 1986).
No unique allozymes have been found in either species (Sene and Carson 1977). The divergence between the species measured with mitochondrial DNA (mtDNA) is approximately 2%, which contrasts with a nearly 7% divergence from an out group species (DeSalle and Giddings 1986).

These species are very similar ecologically and in their courtship displays. Males of *D. silvestris* and *D. heteroneura* have been found displaying in the same patch of woods and even on the same tree fern (Conant 1978). *D. silvestris* tolerates somewhat higher altitudes than *D. heteroneura*; all known populations of *D. heteroneura* are sympatric with *D. silvestris*. The two species differ only slightly in the components of courtship behavior that are visible to humans, that is, they differ in time budgets rather than in the presence or absence of particular behavior patterns (Watson 1979, Boake and Hoikkala 1995, Hoikkala and Welbergen 1995).

In contrast to courtship behavior, however, male aggressive behavior and its associated morphology diverge to a striking extent (Spieth 1981). *D. silvestris* males rear up on their hind legs while shoving each other, but *D. heteroneura* males crouch and push each other with their wide heads (Spieth 1981). Male and female *D. silvestris* have round heads, the norm for members of the genus. Male *D. heteroneura* have stalk eyes that make them appear to have hammerheads (Figure 1). Despite inferences that the broad head is involved in mate choice (Spieth 1981), data that support that inference have been published only recently (Boake et al. 1997).

*D. silvestris* and *D. heteroneura* are capable of producing completely viable and fertile hybrids, but matings between females of *D. heteroneura* and males of *D. silvestris* are rare. The reciprocal cross, which is easy to produce in the laboratory, accounts for all hybrids that have been collected in the field (Carson et al. 1989). This unambiguous behavioral asymmetry has been found in many laboratory tests with these species (Craddock 1974, Val 1977, Spieth 1978, Price and Boake 1995, Fraser and Boake 1997). Thus, although the species are morphologically distinct, they show little genetic divergence, no postzygotic isolation (Ahearn and Templeton 1989), and incomplete behavioral isolation. Clearly, they are still in the process of diverging. Such a pair is ideal for examining how courtship signals contribute to failures to hybridize.

**Investigations of behavioral isolation**

One approach to identifying the traits that contribute to behavioral isolation is to conduct detailed analyses of the courtship behavior of each species, test for differences, and infer that these differences could be involved in speciation. The sequence of courtship identified for *D. silvestris* and *D. heteroneura* is shown in Figure 3. In both species, courtship involves an approach in which the male produces a substrate vibration called a "purr" (Hoy et al. 1988), and one or both in the pair may wave both wings in large vertical circles. The approach is followed by a facing or circling phase in which the male faces the female's head and either backs up as she approaches or circles to her side while continuing...
to purr. Then the male circles all the way behind the female and takes a head-under-wings posture in which his head is close to the tip of her abdomen. If the female does not fly or run away, the male extends both wings laterally and produces a hum by vibrating his wings simultaneously. He then extends his front legs and brushes the sides of her abdomen (Figure 3 does not list this action because it is difficult to verify on a videotape), following which he may attempt to copulate. The female plays an active role in advancing courtship by producing displays that appear to elicit an escalation of courtship from the male; namely, she makes a lunging motion called “slashing” and stands still when the male is in the head-under-wings posture (Boake and Hoikkala 1995, Hoikkala and Welbergen 1995).

Anneli Hoikkala and her colleagues at the University of Oulu in Finland have described the courtship of several planitibia-group species in detail and identified differences among the species (Hoikkala and Kaneshiro 1993, Hoikkala et al. 1994, Hoikkala and Welbergen 1995). Although the general form of courtship is similar for D. silvestris and D. heteroneura, they differ in their airborne and substrate courtship sounds and in the time devoted to the head-under-wings posture and to wing vibration during courtship (Table 1, Figure 3). These observations suggest that the head-under-wings posture or wing vibration could drive reproductive isolation for this pair.

My strategy is to examine courtship in pairings between species, identify the stages at which courtship breaks down, and then investigate these stages experimentally. When Don Price (now at the University of Hawai at Hilo) and I paired D. silvestris males with D. heteroneura females, we found that courtship failed because it did not begin. Males did not reach the head-under-wings or wing-vibration stages; at most, 10% of approaches resulted in courtship. However, once courtship had begun, it was as likely as the reciprocal pairing to result in copulation (Price and Boake 1995). The strong role of the approach stage was surprising: Because of the differences in courtship behavior between the species that Hoikkala had observed (Hoikkala and Welbergen 1995), we had anticipated that wing vibration would be critical. We propose, however, that the earliest stage of courtship is most critical to behavioral isolation, although later stages may also contribute (Price and Boake 1995).

My students and I are now focusing on the approach stage of courtship, which might involve pheromonal signals, substrate vibration, and the broad head. When insect courtship fails to begin, an obvious hypothesis is that pheromones are involved. We are therefore examining the cuticular hydrocarbons of each species in collaboration with a pheromone biochemist. Differences between such hydrocarbons have been implicated in courtship isolation between Drosophila sechellia and Drosophila simulans (Coyne et al. 1994); however, in D. silvestris and D. heteroneura there is no licking or touching of the kind associated with chemical signaling in other Drosophila (Spieth 1978). M. colleagues and I are also examining the purr that males produce during the approach phase of courtship (the purr differs between the species) (Table 1; Hoy et al. 1988, Hoikkala and Welbergen 1995).

We have completed an analysis of the possible role for species differences in head width in behavioral isolation (Boake et al. 1997). The average male head width is 2.8 mm in D. heteroneura and 1.8 mm in D. silvestris. We noted that the first view that a female has of an approaching male is his head; if she could assess its breadth, she would have a simple cue as to the species of the visitor. To determine whether female D. heteroneura are capable of assessing head width in conspecific males, we first tested whether head width is sexually selected within D. heteroneura.

To test for sexual selection within D. heteroneura, we considered both male-male competition and female mating preferences (Boake et al. 1997). The tests of competition involved marking males with a drop of paint on the thorax, then pairing them in an observation chamber and watching them fight; for those pairs that reached the head-shoving level of escalation, we determined the winner (the one that stood his ground) and subsequently measured head widths. In 21 of 25 pairs, the winning male had a broader head, and in three cases the head widths were the same. In only one case did the winner have a smaller head; reexamination of this pair revealed that the losing male had received a big drop of paint on his eye rather than his thorax.

The tests of female behavior involved what are called “no choice” tests, in which a single pair is placed in an observation chamber (Boake et al. 1997). These tests are reasonable for several reasons: First, in the wild the males are so widely dispersed that a female can visit only one at a time, and second, the chambers are large enough to allow females to avoid males if they wish—indeed, we found no evidence of forced copulations, nor have we found all females mating. Over the course of 10 days, each male was given 10 different females; male mating success was scored as the number of females with which he mated. At the end of the behavioral tests, we measured the head width and body size of each male. We found a highly significant correlation between male mating success and head width (P = 0.01) that was independent of body size. Thus, head width is sexually

Table 1. Sounds produced by male Drosophila silvestris and Drosophila heteroneura.\(^a\)

<table>
<thead>
<tr>
<th>Species</th>
<th>Purring Interpulse interval (ms)</th>
<th>Burst length (ms)</th>
<th>Frequency range (Hz)</th>
</tr>
</thead>
<tbody>
<tr>
<td>D. heteroneura</td>
<td>55.0 ± 5.4</td>
<td>8898 ± 3871</td>
<td>120-250</td>
</tr>
<tr>
<td>D. silvestris</td>
<td>46.2 ± 5.6</td>
<td>6668 ± 2511</td>
<td>106-198</td>
</tr>
</tbody>
</table>

\(^a\)Means and standard deviations from at least five males per sample.
selected within *D. heteroneura* through both intermale competition and female mating preferences. Is it involved also in behavioral isolation?

To test for a role of head width in behavioral isolation, we asked whether female *D. heteroneura* failed to mate with male *D. silvestris* because their heads were insufficiently broad. Rather than attempting a surgical manipulation of head width, we took advantage of the fact that the morphological difference between the two species shows a large X-chromosomal effect (Templeton 1977, Val 1977). Reciprocal hybrid males have identical autosomes but differ in the origins of their X chromosomes, as well as in head width (Figure 4). Hybrid males with a *D. heteroneura* mother have broader heads (2.5 mm) than those with a *D. silvestris* mother (1.98 mm). Thus, if head width is the reason that *D. heteroneura* females failed to mate with *D. silvestris* males, the two hybrids should have lower mating success than *D. heteroneura* males, with mating success among the hybrids differing according to their head width. However, we found no differences in mating success when we tested more than 70 males of each of the three genotypes (Figure 5; Boake et al. 1997). Nor did we find any evidence for X-chromosomal influences on the structure of courtship behavior, which could have been a complicating factor (Boake et al. 1998).

These results for head width are inconsistent with the general hypothesis that sexual selection and behavioral isolation form a continuum. Although it is possible that the hypothesis is incorrect, it would be necessary to reject the hypothesis for all relevant sexual signals before it could be decisively rejected for this species pair. We are still testing possible roles for pheromones and substrate vibration. It is also possible that hybrids in the laboratory perform much better than they would in the natural habitat, as has been found for stickleback fishes (Hatfield and Schluter 1999). If that proposition is true, the lack of a difference in mating success between hybrid and *D. heteroneura* males might be an artifact, but the similarity of mating success between the hybrid males would be difficult to ignore because the reciprocal hybrids are autosomally the same. If the general hypothesis is rejected for *D. silvestris* and *D. heteroneura*, the next logical step would be to find out whether it is untrue for other pairs of species. It would be valuable to learn whether there are any taxonomic or ecological factors that would allow us to predict when the hypothesis is likely to be appropriate.

Because we are still testing the other cues that may be involved in the approach that initiates courtship, we cannot conclude that the hypothesis is wrong. Perhaps several cues, operating in a hierarchical fashion, contribute to behavioral isolation (and possibly also to sexual selection). Two hypotheses need to be investigated: First, if other cues are adequate, head width becomes an important cue, as is seen within *D. heteroneura*; and second, other cues may be not merely adequate but capable of overriding the negative effects of a round-headed male, which could explain our results for the F1 hybrid males.

We are also observing postapproach courtship in detail because it may play a role, even if only a secondary one, in behavioral isolation. An obvious candidate for further investigation is the sound produced during wing vibration, which differs between species (Table 1). However, when we examined the intraspecific mating success of males whose wings had been clipped off, thus disabling their sound production, we found no differences between clipped males and unclipped controls (Boake and Poulsen 1997). Similarly, in interspecific pairs, clipped male *D. heteroneura* are as successful as normal males in courting *D. silvestris* females (Christine R. B. Boake, unpublished data).

Readers may have recognized an unsolved question that is clear even from the descriptions at the start of this report. If these species have such weak behavioral barriers and no postzygotic isolation, why are they distinct? The natural hybrids that were found were no more than 2% of all individuals collected (Carson et al. 1989). One hypothesis is that ecological distinctions are stronger than we think. For example, Spieth (1981) noted that *D. heteroneura* tended to be found on perches with brighter light than those on which *D. silvestris* were found. It is also possible that the altitudinal range of *D. heteroneura* used to extend lower than that of *D. silvestris*, but because the native wet forests at lower altitudes have been cleared for agriculture, this hypothesis is untestable. In the mid-1990s I attempted to measure the lighting, temperature, and vegetation density at male perch sites, but the flies had nearly disappeared. They are prey for introduced yellow jackets (*Vespa penysilvica*; Foote and Carson 1995) and their host plants are consumed by feral pigs. Thus, these species are an example of an increasingly common problem in modern biology: the loss of fundamental information about critical issues because of extinction (Grant 2000).

**Conclusions**

I have described a strategy for identifying species differences in courtship and developing experiments to evaluate
their importance to behavioral isolation. Traits that are shown to influence behavioral isolation would then be tested to discover their role in sexual selection. Such studies cannot be used to determine whether sexual selection drove speciation in the past, but they can support or disprove the hypothesis that sexual selection and behavioral isolation are influencing the same traits now. Thus, we can test whether sexual selection and behavioral isolation are parts of a continuum. For this research, it is essential to study pairs of species or populations that are in the process of diverging; otherwise, the observed differences could have evolved after the completion of speciation and not be directly involved in speciation. It is also important to realize that even if two species show a high degree of ecological similarity, as do the subjects of my research, the possible role of ecology in speciation must not be ignored.

A caveat to this research is that it is described as though the females discriminate among potential mates, which is commonly the case in sexual selection. However, we know that in these fly species, male decisions to advance the progress of courtship are influenced by signals that they receive from females (Boake and Hoikkala 1995, Hoikkala and Welbergen 1995). Males of each species will approach anything that is small, dark, and moving (including jumping spiders, with an unfavorable outcome for the fly), but they do not readily advance to the head-under-wings stage even with a conspecific female. Consequently, the phenomenon that is called "behavioral isolation" is likely to involve bidirectional signaling, with males needing appropriate signals from females as much as females need correct signals from males. An advantage of viewing behavioral isolation and sexual selection as parts of a continuum is that we no longer need to consider behavioral isolation as a unique trait; rather, it is a mismatch between the sexual signals that are used by each species. Our goal is to identify the mismatch.

The research described above is part of a larger investigation of the process of speciation. Recent genetic models have focused on the role that sexual selection could play in speciation (Turner and Burrows 1995), while others have addressed contentious issues about the number of genes that could influence speciation (Gavrilets and Hastings 1996). These mathematical models have clear and testable assumptions and predictions. The most appropriate traits with which to test such models are those that have been demonstrated to play a critical role in an ongoing process of speciation, using methods such as the ones described in this article.

Acknowledgments
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Figure 5. Mating success of males of three genotypes with female Drosophila heteroneura (data from Boake et al. 1997). From left to right, the data are from D. heteroneura, the F1 hybrid with D. heteroneura as a mother (HS), and the F1 hybrid with Drosophila silvestris as a mother (SH); differences are not significant at P = 0.05. The mean head widths from left to right are 2.81 mm, 2.5 mm, and 1.98 mm. The sample sizes from left to right are 78, 79, and 75 males.


