Chapter 4
Diversity and Ecology of Stag Beetles (Lucanidae)

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Abstract The beetle family Lucanidae contains over 1200 described species worldwide, with the highest diversity found in Southeast Asia. Most species are saproxylic, with larvae feeding on deadwood at various stages of decomposition and contributing to the breakdown of this material. Female lucanids usually oviposit eggs either directly within decaying wood, at the soil-wood interface beneath logs, or in the soil. Larvae of lucanid beetles spend the majority of their life span living in decaying wood or other decomposing substrates, where they feed on materials rich in fungal biomass. In addition, adults of many lucanid beetles are highly dependent on living trees where either they can find sap as a food source or locate partners for mating. Relatively little is known about the biology, life history, or substrate associations of saproxylic stag beetles despite their striking morphology and popularity among entomologists and amateur insect collectors. In this chapter I discuss ecological niche partitioning among lucanid beetles, with a focus on the relatively well-studied fauna of Taiwan as a case study. I also review the importance of fungal associations to lucanid beetles and the role these insects play in wood decomposition.

4.1 Diversity and Ecology of Stag Beetles

Lucanid beetles are among the largest and most charismatic groups of insects associated with decomposing wood and can serve as important bioindicators of forest integrity. Within a given region, forests with the highest lucanid diversity are generally characterized by lower levels of disturbance and larger amounts of deadwood (Wang 1990; Chang 2006). In Europe, for example, Lachat et al. (2012) reported that lucanids were among the species most sensitive to deadwood amount and temperature among 69 families of saproxylic beetles examined in that study.

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Although most lucanid adults are thought to feed on sap flows and breed in decomposing logs or stumps (Blatchley 1910; Kojima 1996), information about their basic ecology, including host plant associations, is limited. The European giant stag beetle, *Lucanus cervus* (L.), is probably the most well-studied lucanid beetle worldwide, and most studies have focused on its distribution (Thomaes et al. 2008; Harvey et al. 2011a), monitoring and sampling (Harvey et al. 2011b; Chiari et al. 2014; Bardiani et al. 2017), and morphological variation (Clark 1977; Harvey and Gange 2006). Recently, Ulyshen et al. (2017) reported on the basic ecology, genetics, and geographic distribution of the giant stag beetle, *L. elaphus*, in the USA. Tropical and subtropical mature forests in East and Southeast Asia host the highest diversity of lucanid species (Krajcik 2001; Smith 2006), with most published information focusing on new species description and taxonomy (Araya et al. 1998; Han et al. 2010; Zilioli 2012) as well as conservation (Lin et al. 2009; Huang 2014).

4.1.1 Breeding Substrates and Behavior

Most lucanid beetles inhabiting decaying wood feed on cellulosic material highly colonized by fungi and other microorganisms. Although some adult lucanids show strong preferences for the sap of particular host plants, most female lucanids are less discriminating about their selection of breeding substrates (Araya 1993a; Chang 2006). When lucanid females find an appropriate log for oviposition, they will decide how many eggs to lay according to the size and quality of the substrate (Chang 2006). In general, as long as logs are rotten and soft, with adequate humidity and without many termites or other insects, they can provide potentially suitable habitat for oviposition, regardless of whether the log is in contact with the soil or still standing (Chang 2006). Relationship between the decay types (white, brown, and soft rot) in decaying wood and occurrence of lucanid beetles was studied in Japan by Araya (1993a) who found that some lucanid species such as *Ceruchus lignarius* (Lewis) and *Aesalus asiaticus* (Lewis) prefer brown rot and *Platycerus acuticollis* (Kurosawa) is associated with soft rot. However, *P. delicatulus* (Lewis) and other lucanids such as *Prismognathus angularis* (Waterhouse), *Macrodorcas striatipennis* (Motschulsky), *Dorcus montivagus* (Lewis), *D. rubrofemoratus* (Vollenhoven) showed no clear patterns of decay type use. Araya (1993b) further reported that *C. lignarius* occurred exclusively in highly decayed brown rot (brown rot specialist), whereas the occurrence of *P. angularis* was not as clearly associated with either decay type or its stage (decay type generalist).

In Taiwan, females of only a few lucanid species show specificity for particular kinds of decomposing logs for oviposition. For example, *Aegus jengi* is distributed in the northern hills around Taipei City, with adults and larvae being only associated with large pine logs (Huang and Chen 2016). About 10 years ago, with the devastating infection of *Bursaphelenchus xylophilus* (Steiner and Buhrer) vectored by *Monochamus alternatus* (Hope), most pine trees in northern Taiwan were chopped and removed. Although the population and abundance of *A. jengi* has not been officially investigated, such anthropogenic disturbances have the potential to extirpate populations of specialist species.

4.1.2 Larval Ecology and Development

All the known lucanid larvae in Taiwan go through three instars, with the 1st and 2nd instars being relatively brief, usually 2–4 weeks (Chang 2006). The 3rd instar is usually the longest in duration, with most species remaining in this stage for more than half a year and as long as 2 years at cooler elevations. Due to this age structure, most larvae encountered in logs or soil are 3rd instars. Due to the relatively large size of 3rd instar larvae, they typically receive more attention from researchers. However, lack of information about 1st and 2nd instars in the wild results in incomplete knowledge about the development of these species and their importance to decomposition.

Larvae of *Odontolabis siva parryi* (Boileau) and most species in the genus of *Neolucanus* do feed on decaying woody fibrous tissue, but most of the time inhabit in the decomposed soil underneath dead trees. Therefore, adult females often choose rotten roots underneath decaying trees or the undersides of large logs adjacent to the ground for oviposition spots. *Aegus laevicollis formosae* and most *Lucanus* larvae inhabit shallow soil depths where they feed on rich fibrous rotten substrates (Yang 2007). Thus when females of these lucanids find a suitable environment, they will dig into the soil and crawl around to lay eggs. Several genera mentioned above share the same habitat in a specific forest belt, partitioning different niches among logs and the underlying soil to ensure their survivorship and sustainability.

In Australia, different lucanid beetles are reported to utilize white rot, brown rot, drier substrates, sapwood, lower elevation, etc. (Wood et al. 1996). The rainbow stag beetle, *Phalacrognathus muelleri* (Macleay), only breeds in rotting wood in the rainforests of northern Queensland where larvae have been extracted from the wood of 27 tree species in 13 families, all logs experiencing white rot (Wood et al. 1996). In the USA, *Lucanus elaphus* was found in association with a wide range of rot types without any noticeable preference, including white rot, brown rot, and even within veins of relatively intact wood surrounded by rot (Ulyshen et al. 2017).

4.1.3 Fungivory and Symbiotic Microbes

Fungivory is widely observed in insects (Kukor and Martin 1987). Some social insects such as leaf-cutting ants (Hymenoptera) and macrotermitine termites (Blattodea) culture specific fungi in their nests and feed directly on the fungal tissues (Chapela et al. 1994; Wood and Thomas 1989). Some wood-inhabiting insects have endosymbiotic microbes within their guts that help digestion of wood. For example, lower termites and wood-feeding cockroaches have protozoa or bacteria in their digestive organs which produce cellulolytic enzymes (Cleveland 1924; Slaytor 1992; Breznak and Brune 1994). Ambrosia beetles culture and consume ambrosia fungi growing within their galleries in wood (Batra 1963; Beaver 1989). Fungivory is evidently clear for these insect groups. However, for insects that feed on substrates containing fungi, it is difficult to determine if the fungi are used for nutrients or merely consumed along with the substrate. Lucanids, some cerambycid and buprestid beetles, and higher termites inhabit and feed on wood decayed by wood-rotting fungi (Araya 1993a, b; Saint-Germain et al. 2007; Abe et al. 2000). Passalid and cerambycid beetles are associated with xylose-fermenting yeasts that may help in the digestion of wood hemicelluloses (Suh et al. 2003, 2006).

Little is known about what kinds of microbes are associated with stag beetles, although Kuranouchi et al. (2006) indicated the presence of nitrogen-fixing microbes within *Dorcus rectus* (Motschulsky) larvae. Despite their close connection with decomposing wood and associated microbial activity, it remains poorly understood how lucanids interact with fungi and other microorganisms. Wood is composed mostly of cellulose as well as lignin and hemicellulose which together comprise about 90% of the total volume (Parkin 1940). These compounds are difficult to digest and contain low contents of nitrogen, sugars, and starch (Haack and Slansky 1987); such nutrient conditions make wood a poor food resource for insects. Hanula (1996) pointed out five possible advantages of fungal-infested wood over fresh wood as food for insects:

1. Increased concentrations of nitrogen and other elements in fungal mycelia.
2. Increased ingestion and digestion of wood made fragile by wood-rotting fungi.
3. Increased moisture content of wood.
4. Increased digestion of woody tissue by enzymes originating from fungi.
5. Detoxification of toxic or repellent allelochemicals in wood.

Tanahashi et al. (2009) suggested that direct nutrient acquisition from the fungal mycelia may be particularly important. *Dorcus rectus* represents one of the most common and widely distributed stag beetles in Japan (Kurosawa 1985). Tanahashi et al. (2009) reported that adult females of *D. rectus* locate decaying wood of broad-leaved trees affected by white-rot fungi, and it was found that the larvae were able to develop on fungal mycelia without wood; thus, they can be considered fungivorous. This is the first demonstration of fungivory in stag beetles but may be the case for other species as well.

Some fungivorous insects possess a mycangium (pl. mycangia), a special structure on the body in which symbiotic fungi (usually in spore form) are transported to new locations (Beaver 1989). Mycangia have evolved in a number of beetle lineages including multiple times in Scolytinae (Curculionidae) and lymexylids. In some cases, as in ambrosia beetles, the fungi are cultivated for food on the gallery walls. In other cases, such as the southern pine beetle, *Dendroctonus frontalis* Zimmermann, phloem is the main food, and fungi weaken the defense response from host plant (Six and Wingfield 2011).

Tanahashi et al. (2010) further reported the first evidence of a mycangium in lucanids which is located near the dorsal side of the rectum in the abdomen.

Interestingly, there was no mycangium near the rectums of any male lucanid or of either sex in the sampled passalid, geotrupid, and scarabaeid species, which are families of beetles closely related to Lucanidae (Smith et al. 2006). Yeastlike microbes, closely related to the xylose-fermenting yeasts *Pichia stipitis* Pignal, *P. segobiensis* Santa María and García Aser, or *P.* sp., were isolated from the mycangium of five lucanid species (Tanahashi et al. 2010). The larvae of the five lucanid species from which xylose-fermenting yeasts were isolated in that study exclusively feed on wood colonized by white-rot fungi. *Dorcus rectus* and *D. striatipennis* (Motschulsky) are white-rot specialists, and three other species, *D. titanus sakishimanus* (Nomura), *Prosopocoilus pseudodissimilis* (Kurosawa), and *Prismognathus angularis* (Waterhouse), are somewhat less specialized. Although not confirmed, Tanahashi and Fremlin (2013) proposed that ovipositing female stag beetles may inoculate the substrate with their mycangium yeasts. If so, this is potentially another example of parental care behavior. The absence of mycangia in passalids may be explained by the subsocial behavior of this group, where adults help prepare food for developing larvae (Tanahashi et al. 2010). Moreover, whereas passalid adults and larvae both feed on decomposing wood, lucanid adults are primarily sap feeders and may thus lack the gut microbes needed in the larval stage to digest wood (Tanahashi et al. 2010). Inoculating oviposition sites with xylose-fermenting yeasts from mycangia may thus be a way for female lucanids to help their offspring digest wood. More research is needed to explore these possibilities.

4.1.4 Parental Care

Parental care is thought to be one of the key factors in the evolution of social behavior and is favored in situations characterized by ephemeral resources (Bartlett and Ashworth 1988), nesting systems relatively safe from predators (Scott 1990), or situations where finding and establishing a new nesting system may be difficult and dangerous (Kirkendall et al. 1997). In Japan, it was found that the initial growth rate of 3rd instar *Figulus binodulus* (Waterhouse) was significantly higher when the larvae were in a nest with adults compared to those in a nest without adults (Mori and Chiba 2009). Their results suggest that *F. binodulus* has a level of sociality and nest mate recognition that is very rare in stag beetles (Mori and Chiba 2009). In Taiwan, females of all species of *Figulus*, several species of *Aegus*, and *Nigidionus parryi* (Bates) usually burrow into the log using their mandibles and stay inside the log laying eggs in the rotten substrates until they die. *Nigidionus parryi* especially shows “parental care” as most larvae found in the decaying logs coexist with adults (Chang 2006).

4.2 Niche Partitioning of Lucanids in Taiwan

4.2.1 Diversity and Environment of the Taiwan Island

Taiwan is unique among all subtropical regions because it is the only sizeable island located immediately north or south of the tropical zone between the 23rd parallels (Huang and Lin 2010). The island is unique for its complex terrain, from low altitude coastal plains to a Central Mountain Range (CMR) containing more than 200 peaks exceeding 3000 m elevation (Huang et al. 2006). Forests in Taiwan can be categorized as the tropical monsoon forest, the subtropical forest, and the temperate grassland. Su (1992) categorized seven forest belts based on the seven different climate zones with their corresponding elevation (Table 4.1). The island contains more than 4000 native plant species, and a quarter (1054 species) of them are endemic (Su 1984). The number of insect species recorded in Taiwan is about 2% of the world's total, but the total land area of the island accounts for only 0.25% of the global total. There are nearly 5000 kinds of beetles in Taiwan, including at least 55 described species of Lucanidae (Chang 2006; Huang and Chen 2015, 2016) (Table 4.2). Taiwan thus contains nearly one twentieth of the 1200 lucanid species known globally. By contrast, the neighboring country of Japan, which has more than a tenfold larger land area, has just 40 species of lucanids. On the other side of the Pacific Ocean, North America harbors only 24 lucanid species, but the total area is near 700 times larger than the Taiwan Island. The lucanid fauna of Taiwan is not only diverse but also relatively well-studied, providing an excellent opportunity to gain insights into the ecology of this group of insects.

Among the 55 lucanid species in Taiwan (Fig. 4.1), all of them are found from tropical to temperate zones below 2800 m in elevation, and most species are restricted to a specific vegetation zone (Chang 2006). The absence of species above 3000 m is presumably due to the low temperatures and low floral diversity associated with the cool temperate to subarctic zones. Except for some species of *Lucanus* that are speculated to feed on grass roots, most lucanids in Taiwan are considered saproxylic as the larvae feed directly on decomposing woody substrates or rotten soil that contains highly decomposed wood such as the genus *Neolucanus* (Table 4.2). Ecological niches among lucanids in Taiwan are discussed mainly based on forest belt (climate niche) and host plants (food niche).

Table 4.1 Taiwan flora category with the corresponding climate zone and elevation

Climate zone	Flora belt	Elevation (m)
Subarctic zone	Alpine vegetation	>3600
Cold temperate zone	*Abies* zone	3100–3600
Cool temperate zone	*Tsuga-Picea* zone	2500–3100
Temperate zone	*Quercus* zone (upper)	2000–2500
Warm temperate zone	*Quercus* zone (lower)	1500–2000
Subtropical zone	*Machilus-Castanopsis* zone	500–1500
Tropical zone	*Ficus-Machilus* zone	<500

Table 4.2 Lucanid species known from Taiwan and their substrate associations

Genus/species	Distribution (flora belt)	Breeding substrate (wood/soil)	Rot type
Aegus			
Aegus laevicollis formosae Bates	*Machilus-Castanopsis–Quercus* (lower)	Decomposed soil	Brown rot
Aegus jengi (Huang and Chen)	*Machilus-Castanopsis*	Decomposed pine	Brown rot
Aegus kurosawai Okajima and Ichikawa	*Quercus* (upper and lower)	Decomposed pine mud	Brown rot
Aegus chelifer Macleay	*Ficus-Machilus*	Decomposed wood	Brown rot
Aesalus			
Aesalus imanishii Inahara and Ratti	*Quercus* (upper and lower)	Decomposed conifer	Brown rot
Cyclommatus			
Cyclommatus scutellaris Mollenkamp	*Ficus-Machilus–Machilus-Castanopsis*	Decaying hardwood	White rot
Cyclommatus asahinai Kurosawa	*Machilus-Castanopsis–Quercus* (lower)	Decaying hardwood	White rot
Cyclommatus mniszechi Thomson	*Ficus-Machilus–Machilus-Castanopsis*	Decaying hardwood	White rot
Dorcus			
Dorcus grandis formosanus Miwa	*Ficus-Machilus–Machilus-Castanopsis*	Decaying hardwood	White rot
Dorcus schenkingi Mollenkamp	*Machilus-Castanopsis–Quercus* (lower)	Decaying hardwood	White rot
Dorcus miwai Benesh	*Machilus-Castanopsis–Quercus* (upper and lower)	Decaying hardwood	White rot
Dorcus yamadai Miwa	*Machilus-Castanopsis–Quercus* (upper and lower)	Decaying hardwood	White rot
Dorcus titanus sika Kriesche	*Ficus-Machilus–Machilus-Castanopsis*	Decaying hardwood	Generalist
Dorcus kyanrauensis Miwa	*Ficus-Machilus–Quercus* (lower)	Decaying hardwood	Generalist
Dorcus parvulus Hope and Westwood	*Ficus-Machilus*	Decaying hardwood	Generalist
Dorcus reichei clypeatus Benesh	*Machilus-Castanopsis–Quercus* (upper and lower)	Decaying hardwood	White rot
Dorcus gracilicornis Benesh	*Machilus-Castanopsis–Quercus* (upper and lower)	Decaying hardwood	White rot
Dorcus mochizukii Miwa	*Machilus-Castanopsis–Quercus* (upper and lower)	Decaying hardwood	White rot
Dorcus rectus Motschulsky	*Machilus-Castanopsis–Quercus* (lower)	Decaying hardwood	White rot
Dorcus striatipennis yushiroi Sakaino	*Quercus* (upper and lower)	Decaying hardwood	White rot
Dorcus taiwanicus Nakane and Makino	*Machilus-Castanopsis–Quercus* (lower)	Decaying hardwood	White rot

(continued)

Table 4.2 (continued)

Genus/species	Distribution (flora belt)	Breeding substrate (wood/soil)	Rot type
Dorcus carinulatus Nagel	*Machilus-Castanopsis–Quercus* (lower)	Decaying hardwood	White rot
Echinoaesalus			
Echinoaesalus chungi Huang and Chen	*Ficus-Machilus*	Decaying hardwood	Unknown
Figulus			
Figulus binodulus Waterhouse	*Ficus-Machilus–Machilus-Castanopsis*	Decaying hardwood	White rot
Figulus punctatus Waterhouse	*Ficus-Machilus*	Decaying hardwood	Unknown
Figulus curvicornis Benesh	*Ficus-Machilus*	Decaying hardwood	Unknown
Figulus fissicollis Fairmaire	*Ficus-Machilus*	Decaying hardwood	Unknown
Lucanus			
Lucanus formosanus Planet	*Machilus-Castanopsis*	Decomposed soil	Brown rot
Lucanus maculifemoratus taiwanus Miwa	*Machilus-Castanopsis–Quercus* (upper and lower)	Decomposed soil	Brown rot
Lucanus swinhoei Parry	*Ficus-Machilus–Quercus* (upper)	Decomposed soil	Unknown
Lucanus datunensis Hashimoto	*Machilus-Castanopsis*	Decomposed soil in bottom grassland	Unknown
Lucanus kanoi Kurosawa	*Machilus-Castanopsis–Quercus* (upper and lower)	Decomposed soil	Brown rot
Lucanus kurosawai Sakaino	*Quercus* (upper and lower)	Decomposed soil	Brown rot
Lucanus miwai Kurosawa	*Quercus* (upper and lower)	Decomposed soil	Brown rot
Lucanus ogakii Imanishi	*Quercus* (upper and lower)	Decomposed soil	Brown rot
Neolucanus			
Neolucanus swinhoei Bates	*Ficus-Machilus–Machilus-Castanopsis*	Decomposed soil	Brown rot
Neolucanus maximus vendli Dudich	*Machilus-Castanopsis–Quercus* (lower)	Decomposed soil	Brown rot
Neolucanus eugeniae Bomans	*Machilus-Castanopsis*	Decomposed soil	Unknown
Neolucanus doro Mizunuma	*Machilus-Castanopsis–Quercus* (lower)	Decomposed soil	Brown rot
Neolucanus sinicus formosanus Mizunuma	*Ficus-Machilus–Machilus-Castanopsis*	Decomposed soil	Unknown
Nigidionus			
Nigidionus parryi Bates	*Machilus-Castanopsis*	Decaying hardwood	White rot

(continued)

Table 4.2 (continued)

Genus/species	Distribution (flora belt)	Breeding substrate (wood/soil)	Rot type
Nigidius			
Nigidius acutangulus Heller	*Machilus-Castanopsis*	Decaying hardwood	Unknown
Nigidius baeri Boileau	*Ficus-Machilus*	Decaying hardwood	Brown rot
Nigidius formosanus Bates	*Ficus-Machilus*	Decaying hardwood	White rot
Nigidius lewisi Boileau	*Ficus-Machilus–Machilus-Castanopsis*	Decaying hardwood	Unknown
Odontolabis			
Odontolabis siva parryi Boileau	*Ficus-Machilus–Machilus-Castanopsis*	Decomposed soil	Brown rot
Prismognathus			
Prismognathus formosanus Nagel	*Quercus* (upper and lower)	Decaying hardwood	White rot
Prismognathus piluensis Sakaino	*Quercus* (upper and lower)	Decaying hardwood	White rot
Prismognathus davidis Bomans and Ratti	*Quercus* (upper and lower)	Decaying hardwood	White rot
Prosopocoilus			
Prosopocoilus astacoides blanchardi Parry	*Ficus-Machilus–Quercus* (lower)	Unknown	Unknown
Prosopocoilus forficula austerus DeLisle	*Ficus-Machilus–Machilus-Castanopsis*	Decaying hardwood	White rot
Prosopocoilus motschulskii Waterhouse	*Ficus-Machilus*	Decomposed soil	Unknown
Prosopocoilus formosanus Miwa	*Machilus-Castanopsis–Quercus* (lower)	Decaying hardwood	White rot
Pseudorhaetus			
Pseudorhaetus sinicus concolor Benesh	*Machilus-Castanopsis*	Decaying hardwood	White rot
Rhaetulus			
Rhaetulus crenatus Westwood	*Ficus-Machilus–Machilus-Castanopsis*	Decaying hardwood	Generalist

4.2.2 *Lucanus*

The lower and upper *Quercus* zones, together ranging from 1500 to 2500 m, contain the most well-protected forest habitats for lucanid beetles in Taiwan. These *Quercus* forests are generally given protected status by the government as national parks or preserves, thus providing relatively less disturbed conditions for a diverse lucanid assemblage. *Lucanus* is the typical genus of lucanids living in this temperate *Quercus* zone. In the upper *Quercus* forest, the distributions of *Lucanus maculifemoratus taiwanus* Miwa, *L. swinhoei* Parry, *L. kanoi* Kurosawa,

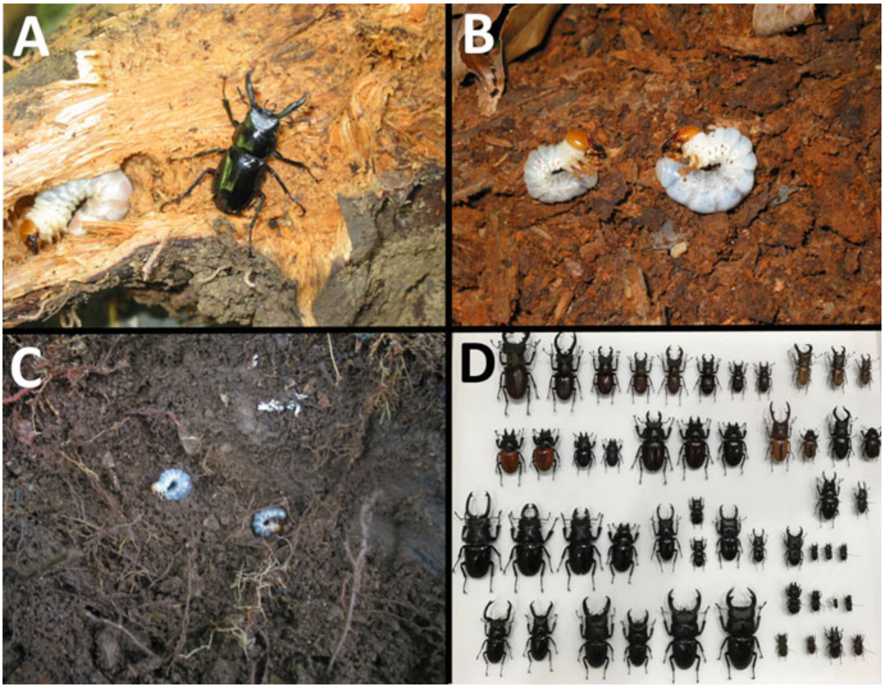

Fig. 4.1 Lucanid beetle larvae and associated feeding environment: (**a**) adult and 3rd instar larva of *Pseudorhaetus sinicus* associated with white rot; (**b**) larvae of *Neolucanus maximus vendli* associated with brown rot; (**c**) 3rd instar larvae of *Lucanus kurosawai* associated with decomposed soil; (**d**) lucanid diversity in Taiwan

L. kurosawai Sakaino, and *L. miwai* Kurosawa could overlap in certain areas (elevation, 1800–2300 m) of the Central Mountain Range (Chang 2006). These lucanids can be found together in mature forests with one species more numerous than the others, depending on the location. It is believed that these lucanid species share the same habitat and utilize similar food sources in the larval stage, all feeding on decaying rotten wood or soil substrates. The degree of rottenness might be an important factor in determining where females choose to oviposit. In artificial rearing chambers, most *Lucanus* females will lay eggs in fermented rotten soil made from saw dust of *Quercus* trees (Lai 2001). However, more eggs can be found between soil surface and decayed wood when given additional material (e.g., piece of decayed maple wood) for oviposition (Lai 2001). Interestingly, these *Lucanus* larvae were never found in living trees or dead dry logs without any moisture in the wild. This may explain that these *Lucanus* can feed on decaying *Quercus* wood in general, but the degree of decaying might be the key for females to determine where to lay eggs. In the USA, Ulyshen et al. (2017) reported the substrates within which *L. elaphus* (Fabricius) were found feeding were always damp and sometimes thoroughly saturated. Drier wood, as sampled at upland sites or in logs with limited ground contact, never yielded *L. elaphus* (Ulyshen et al. 2017).

Niche partitioning among lucanid larvae remains far from understood which requires more research to explore the ecology of oviposition behavior.

Some lucanid species can be found in several vegetation zones, suggesting a high degree of flexibility with respect to both adult and larval plant associations. *Lucanus swinhoei*, for example, can be found in subtropical and warm temperate (i.e., lower *Quercus*) zones and appears to behave differently in the different areas. Within the lower *Quercus* zone, for example, adults of *L. swinhoei* associate strongly with *Quercus variabilis* (Blume), commonly feeding on sap flows during the daytime and rarely coming to lights at night. *Lucanus swinhoei* also occurs within the *Ficus-Machilus* zone (<200 m in the northern coastal hills), where *Q. variabilis* does not occur; instead, the dominant plants are *Acacia confusa* Merr., *Sapium sebiferum* (L.) Roxb., and Lauraceae. In addition, adults of *L. swinhoei* in this region are strongly attracted to lights at night. How *L. swinhoei* has adapted to these highly dissimilar climates and plant communities remains a question for enthusiasts or ecologists to answer. On the other hand, a related species, *L. maculifemoratus taiwanus*, inhabits the same *Quercus* zone in CMR but never occurs down to *Ficus-Machilus* zone in northern coastal hills (Chang 2006).

Another classic example is the endemic lucanid *L. formosanus* Planet. Adults of *L. formosanus* exhibit a strong association with *Cyclobalanopsis glauca* (Thunb) distributed in *Machilus-Castanopsis* zone. Adults of *L. formosanus* often rest in the canopy of *C. glauca* where there is an availability of sap flow on trunks and branches. A clear preference for the canopy layer of *L. formosanus* is similar to *L. cervus* and *L. elaphus*, the two large *Lucanus* species occurring in Europe and the USA, respectively (Bardiani et al. 2017; Ulyshen et al. 2017). Larvae of *L. formosanus* can also be found feeding on rotten soil substrate beneath logs similar to other members of *Lucanus*. Ulyshen et al. (2017) also indicated larvae of *L. elaphus* were found either tunneling inside logs or feeding beneath logs at the soil-wood interface.

One that exhibits a completely different ecology from other *Lucanus* is *L. datunensis* (Hashimoto). Its distribution is limited to the hilltop area of Daiton Mountain (elevation 800–1100 m) located in Yangmingshan National Park in Taipei City (Lin et al. 2009). Interestingly, although this area is within *Machilus-Castanopsis* zone, there is no hardwood forest locally due to severe winter and northeast monsoon. Instead, only two grasses dominate this habitat, dwarf bamboo [*Pseudosasa usawai* (Hayata.) Makino & Nemoto.] and Japanese silver grass [*Miscanthus floridulus* (Labill.) Warb. ex K. Schum. & Lauterb.], with some Azaleas and *Eupatorium shimadae* (Kitam.) growing along the roadside. Males of *L. datunensis* often fly in the daytime around the grassland hovering up and down among grasses seeking mates; females are rarely found and probably spend most of the time near their breeding substrates at the bases of grasses. Lin et al. (2009) hypothesize that diurnal mate searching and the small size of *L. datunensis* are both adaptations in response to a habitat shift from forests to grasslands. Although there have been no field observations of larval *L. datunensis*, it is speculated that *L. datunensis* feed on the rotten soil under the two grass species (Chang 2006). Due to the extremely limited distribution, Lin et al. (2009) proposed that protection and restoration of the grassland habitat consisting of the dwarf bamboo and Japanese silver grass in Yangmingshan National Park should be a top priority for developing a conservation strategy for the threatened *L. datunensis*.

Another daytime-active *Lucanus* is *L. miwai*; it inhabits in the *Quercus* zone in CMR overlapping with *L. maculifemoratus taiwanus*, *L. swinhoei*, *L. kanoi*, and *L. kurosawai*. Males of *L. miwai* hover up and down along the edge of forests or grassy areas on warm spring (April–May) days looking for mates (Wang 1990; Huang 2014), a flying behavior similar to *L. datunensis*. It is noteworthy that both *L. miwai* and *L. datunensis* are only active in the daytime and are never attracted to lights at night, contrasting with the nocturnal habits of the other four *Lucanus* species found in the same habitat. Males of many lucanid species possess curving and greatly enlarged mandibles that often are used in male-male competition for access to females (Clark 1977; Kawano 1992). The active diurnal mate searching flight in open fields in these two species may result in a better strategy over a more widespread behavior of intra-sex competition for resources and mating found in most forest-dwelling lucanids (Harvey and Gange 2006; Rink and Sinsch 2007; Lin et al. 2009). Diurnal activity has also been observed in other lucanids. In Brazil, all members of the genus *Leptinopterus* have diurnal habits and have been collected flying or feeding at sap flows of trees and shrubs (Grossi 2009).

Spatial niche is also partitioned among these *Lucanus* species. Although they are present within the same vegetation zone, the distributions of the various *Lucanus* species differ slightly in terms of altitude. In general, *L. kurosawai* occurs at the highest elevations, followed by *L. miwai*, *L. kanoi*, *L. maculifemoratus taiwanus*, and *L. swinhoei* in the Central Mountain Range. While some species can be found at a wide range of elevations (*L. maculifemoratus taiwanus* and *L. swinhoei*), the altitudinal distributions of other species are more restricted (*L. kurosawai*, *L. miwai* and *L. kanoi*) (Chang 2006; Yang 2007).

4.2.3 Aegus

Niche partitioning is well documented among the four species of *Aegus* found in Taiwan. *Aegus laevicollis formosae* (Bates) occurs across a broad range of elevation from 500 to 2000 m in Taiwan. Adults of *A. laevicollis formosae* are often seen feeding on tree flows of *Acacia confusa* (Merr.) and *C. glauca*. Larvae of *A. laevicollis formosae* were found in rotten substrates under *Miscanthus* or *Fargesia* logs. *Aegus jengi* (Huang and Chen) occurs in the *Machilus-Castanopsis* zone of northern Taiwan, with larvae often found in reddish rotten pine wood, especially *Pinus taiwanensis* (Hayata) (Chang 2006). Adults are seldom observed outside away from breeding substrates. *Aegus kurosawai* (Okajima and Ichikawa) also utilizes highly decomposed pine wood that is often mud-like in consistency but occurs at higher elevations in the *Quercus* zone (1600–2600 m). *Aegus chelifer* (Macleay) is the only *Aegus* species not living in mountain ranges; instead, they are only found in deadwood in coastal areas where they are attracted to lights. It is believed that *A. chelifer* was introduced to Taiwan through the movement of wood from South Asia, and populations of the species have since become well established in certain coastal areas.

4.2.4 Neolucanus

Species of the genus *Neolucanus* prefer to feed on completely decomposed rotten soil substrates, e.g., under logs in broadleaf forests. *Neolucanus swinhoei* (Bates) is diurnally active and is commonly found walking on roadsides or hanging on trees in the *Ficus-Machilus* and *Machilus-Castanopsis* zones. *Neolucanus doro* (Mizunuma) occurs at relatively higher elevations from the *Machilus-Castanopsis* to lower *Quercus* zones and is also diurnal, often seen walking on trails or roads similar to *N. swinhoei* (Chang 2006). *Neolucanus maximus vendli* (Dudich) also occurs within the same forest belt between the *Machilus-Castanopsis* and lower *Quercus* zones but is active at night, and adults can be attracted to lights after 10 pm. However, *N. maximus vendli* can also be found in the daytime feeding on tree flows in the forest canopy (Chang 2006). Larvae of *N. maximus vendli* are found in red rotten soil underneath big decaying trunks or dead roots. Temporal and spatial niche partitioning is demonstrated between *N. doro* and *N. maximus vendli*, presumably a strategy for these species to avoid interspecific competition while sharing the same habitat.

4.3 Threats to Lucanid Diversity and Future Recommendation

In Japan, the wild populations of native stag beetles are rapidly decreasing because of artificial disturbance of habitats, and some species are already close to endangered (Kojima 2003). It has been reported that Southeast Asia has the highest relative rate of deforestation of any major tropical region and could lose three quarters of its original forests by 2100 and up to 42% of its biodiversity (Sodhi et al. 2004). Recent research has highlighted the sensitivity of saproxylic insects to forest management, with managed or secondary forests generally supporting fewer individuals, fewer species, and different assemblages compared to old-growth or primary forests (Grove 2002). Habitat loss in recent years has been an unsolved issue that will ultimately lead to extinction of species, including lucanid beetles that are highly dependent on forest and logs. Meanwhile, biological invasions by exotic stag beetles may also pose a threat to native lucanid populations (Goka et al. 2004). It is believed that the first impact will be competition for food and habitat, the second, genetic introgression as a consequence of hybridization between exotic and native species, and the third, invasion of imported parasites (Goka et al. 2004). In Japan, Kanzaki et al. (2011) reported that eight species of nematodes were cultured from eight species of lucanid beetles, including four phoretic nematodes considered to predominate. The nematodes exhibited low host specificity and were widely distributed. Global trading of lucanids among hobbyists thus risks the introduction of exotic nematodes in Japan and elsewhere, with the potential to be then passed on to native lucanid populations where they can potentially hybridize or otherwise disrupt native nematode populations (Kanzaki et al. 2011).

Due to their relatively large size and to the greatly exaggerated mandibles of many species, stag beetles are among the most enthusiastically collected insect groups by amateur collectors and insect vendors (Goka et al. 2004). The market size of the stag beetle commerce is considered to be over 10 billion Japanese yen (USD100 million) (Goka et al. 2004), involving 700 lucanid species from all over the world with over 15 million specimens imported to Japan each year (Tournant et al. 2012). Mass capturing for commercial purposes, exotic invasion from global trading, and destruction of suitable habitats by human activities inevitably threaten stag beetle populations and their long-term survival (Speight 1989; Berg et al. 1994).

Since 2015, the Taiwanese government implemented a comprehensive replacement of street lights from mercury light bulbs to LED lights throughout the island to save energy. This action incidentally saved millions of lucanids and other nocturnal beetles attracted to mercury street lights at night and killed by vehicles, especially in mountainous areas. Ultimately, in order to protect saproxylic insects like lucanid beetles, efforts to preserve their original habitats are no doubt the best practice. Minimizing anthropogenic exploitation, prohibiting or limiting logging activities, and preserving natural habitats will together promote the long-term conservation of lucanid beetles.

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