INSECT COLORATION AND IMPLICATIONS FOR CONSERVATION

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ABSTRACT

Large, conspicuously colored insect taxa, due to associated logistical and anthropocentric biases in knowledge, public support and legislative consideration, are favored as targets of species protection, environmental monitors and education tools. They are also vulnerable to collection and perhaps, due to ecological specializations associated with apparency, to extinction. I discuss the implications for conservation.

Key Words: insect conservation, insect coloration, insect apparency, insect conservation policy

RESUMEN

La taxa de insectos grandes y visiblemente coloreados, por estar asociados a prejuicios en el conocimiento antropocéntrico y logístico, apoyo público y consideración legal, son favorecidos como blanco por grupos dedicados a la protección de especies, a monitorear el medio ambiente y a utilizarlos como herramienta educativa. Estos insectos también son vulnerables a la colección y quizás, debido a especializaciones ecológicas asociadas con la apariencia, también son vulnerables a la extinción. Se discuten las implicaciones en términos de conservación.

Insects dominate terrestrial ecosystems in terms of species, biomass, number of individuals, and importance of ecological roles (Ricklefs et al. 1984, Wilson 1987, 1988). Approximately 80% of all described metazoan species are insects (Samways 1992). Insect global distribution is highly biased, with over 50% living on less than 7% of the earth's surface in tropical rain forests (Samways 1994). It has been estimated that only about 5% of insect species have been described, and significant information is thought to exist on less than 1% of these (Raven 1990). Almost all of that information has been garnered from either pest or charismatic species in temperate areas; neither are representative samples of insect biological diversity.

Insects are susceptible to the same anthropogenic threats as vertebrates. Wilson (1988) estimates that species extinctions are occurring at a rate of at least 1000 times faster than before human-induced extinction pressures. However, most insect population declines and extinctions go unnoticed or unappreciated. This is largely a result of apparency-related obstacles. Small size and inconspicuous habits, together with tremendous diversity and a mostly tropical distribution, make insects largely invisible to human attention and concern.

Humans most readily learn about, care about, and make sacrifices for animals that are apparent, familiar, aesthetically appealing, and demonstrate positive benefits to mankind. Such glamorous species often enjoy special privileges in species-oriented conservation efforts, due to research, funding, and political and public support. On the other hand, they may be particularly susceptible to anthropogenic impacts, directly through their status as commodities and indirectly through special ecological needs associated with their apparency. Familiar and appealing insects also offer special advantages for larger-than-species-scale conservation efforts. Existing historical and ecological knowledge, sampling methodologies, expert interest, and financial support enhance the use of glamorous species as indicators of biological diversity and as monitors of environmental change.

Animal apparency and aesthetic appeal are related to their coloration, morphology, behavior, and size. Strikingly colored, shaped, or behaviorally interesting creatures benefit from heightened conservation attention. However, with regard to insects, size is a limiting factor. Glamor status occurs only when a species is large enough 1) to be well-studied and sampled, and 2) to overcome anthropocentric biases that favor larger animals. Such threshold sizes are atypical of insects; by far, most insects are minute or small. In North America, described insect species vary from less than 1 mm to approximately 15 cm, with more than half being less than 6 mm long (Borror & White 1970). Of approximately 430 species of adult beetles collected by fogging in four tropical forests in Brazil, 97% were less than 8 mm in length (Erwin 1983). Although speciose groups, including Coleoptera, Lepidoptera and Diptera, contain some of the largest, most well-studied and charismatic species, flamboyance is not typical even within these taxa.

I will briefly discuss the roles of the environment, life history strategies, sexual selection and predator defense in shaping adaptations associated with apparency and beauty in insects. I will then consider how these adaptations influence 1) the way we value species, 2) anthropogenic threats to their populations, and 3) how we treat species in conservation policy and management.

Sources of Variation in Apparency and Aesthetic Appeal, and Implications for Conservation

Sources of variation in apparency and aesthetic appeal in insects include adaptations associated with the environment, particular life history strategies, predator defense, sexual selection, and the interplay of these. Population and species differences in size, shape, and coloration can reflect variation in temperature, humidity, and daylength. Differing ecotypes contain species with characteristic arrays of adaptations that influence diversity at all levels of biological organization. For example, tundra ecosystem thermal and daylight constraints and structural simplicity limit within and among species variation. Few species are naturally rare. Such environments and their relatively uneventful insect species are seldom the focus of conservation efforts. Only under larger-scale efforts that focus on preservation of representative ecotypes are such landscapes and species given significant conservation attention. On the other hand, tropical areas are generally characterized by seasonally stable, structurally complex environments, and strong biotic selective pressures. Intra- and interspecific diversity is extreme in size, coloration, and associated behaviors, habitat specialization, and distribution patterns. Such environments receive high conservation priority. Ironically, these areas represent our greatest conservation challenges specifically because such extreme variation eludes current conservation strategies.

Phenotypic variation can occur through the season or through a species' range and can be genetic and/or environmentally controlled. The nature of this control is important in conservation theory and practice. Color polymorphisms can be sources of biological diversity (Samways 1994), sources of confusion in monitoring populations (Crother 1992), and focuses of interest for researchers and collectors. Differing color forms can be associated with differing macro- or micro-habitat preferences affecting within-species vulnerabilities to anthropogenic changes to the environment. For example, the peppered moth (*Biston betularia*) demonstrates how genetic polymorphisms in color, form and associated resting surface preferences can lead to color form-specific responses to human-induced changes to the environment.

Where biological variation over space is relatively gradual, conservation efforts are often directed at range extremes. These areas are often marked by apparency-related characters. Variation in insect color, morphology, behavior and size are also used to map areas of abrupt environmental change, increased variability within and among species, and speciation hot spots.

Complex life cycles are common in insects, especially speciose taxa with large, readily apparent species such as Coleoptera, Lepidoptera, and Diptera. Variation in appearance and ecological specialization associated with different life stages can be extreme and influence both our concern and our ability to conserve species. Extreme differences in life stage forms can lead to conflicts of interest, taxonomic confusion and a need for increased research efforts.

Insect size and coloration are integral parts of life history strategies that are associated with factors such as mobility, longevity, degree of habitat specialization, activity periods, flight patterns, predator avoidance, and feeding strategies. For example, reproductive rate is related to insect size. Some of the largest and most dramatically colored insects, such as the birdwings (*Ornithoptera*, Papilionidae), are considered K-selected species. Because such long-lived species produce relatively few eggs at a low rate, they can be especially vulnerable to extinction. Furthermore, large, conspicuous species often live in closed or sedentary populations that are thought to be especially threatened by habitat fragmentation (Thomas 1984, Thomas & Mallorie 1985).

Large, conspicuous species, due to their associated ecological specializations, may exist as groups of local sub-populations. Such metapopulations are potentially buffered from extinction within an area by re-colonization from surrounding sub-populations. Such populations may by particularly vulnerable to habitat destruction and require regional approaches to their conservation (Murphy et al. 1990). Metapopulations are thought to be common in insects in general and differ from those used to develop vertebrate models used in population viability assessments and recovery plans (Murphy et al. 1990).

Insect apparency is increased when aggregations are formed in association with roosting, feeding, mating, predator defense, moderation of the environment, or overwintering. Such aggregations increase the apparency of the group to potential predators and to collectors. Insect behavior and aggregation site characteristics may further increase exposure. For example, swarming or hilltopping mating aggregations often occur in exposed locales and individuals remain in flight almost constantly. Although long-term aggregations associated with warning coloration may function to deter predation (Vulinec 1990), they may be especially vulnerable to collection due to the increased accessibility and the economic value associated with aposematism. When aggregations involve a large portion of the population for an extended time, their members become especially vulnerable to very specific habitat threats.

At least in tropical butterflies, aggregations are associated with other life-history strategies, such as restricted home ranges, low reproductive rates, and increased longevity (Turner 1975), that magnify their vulnerability to human-induced threats to their habitat. Congregated organisms also bias our perception and measurement of rarity, thereby favoring aggregated species and populations in conservation priority rankings.

Predation pressures not only impact conservation efforts through the evolution of aggregation behavior, but as selection agents in the evolution of warning coloration, concealment, crypsis, and mimicry. Depending on the adaptation and the particular threat faced, these adaptations may benefit or harm the conservation of a species. For example, insects that rely on concealment or blend into their background are often small and drab. While such adaptations may lessen potential anthropogenic threats such as insect collection, inconspicuous species are not likely to be well-studied and their conservation is unlikely to gain public support. Because their inconspicuousness is dependent on specific associations with a component of the insect's environment, these insects can be especially vulnerable to changes in their habitat. Cryptic species that mimic a particular object such as a leaf, due to their often exposed resting and feeding habits and their associated low population densities, may be particularly vulnerable to climate change, pollution, and pesticides. Furthermore, once discovered by collectors, cryptic species may become economically valued due to their aesthetic intrigue. For the same reason, they may also gain research favor and public support.

Chemically protected aposematic insects are thought to have evolved bright, bold coloration, often involving black, yellow, orange or red, as an advertisement of their unpalatability to visual predators such as birds and lizards. Aposematic insects are among the most-valued aesthetically, the most-studied, and the most-exploited in trade largely because human visual systems are also attuned to such colors and patterns.

Such species often attain their chemical protection by sequestering secondary substances produced by plants as adaptations against phytophagous insects. Plant and insect counter-adaptations lead to very specific and dependent relationships. Such co-adaptations increase insect vulnerability due to the indirect impacts of disruptions to their associated plant ecology. Insect-plant associations can restrict geographical and ecological tolerance increasing susceptibility to climate change (Samways 1994). Batesian and Mullerian mimicry complexes are commonly associated with warningly colored insects. These complexes can be confusing taxonomically. Because of scientific interest in using mimicry complexes as tools to understand ecology and evolution, the associated species are often some of the best understood ecologically and genetically. Their apparency also enhances the practicality of their study.

Sexual selection pressures account for many adaptations that we associate with beauty in insects, and why we often prize males as commodities. Secondary sexual characters that function in intrasexual interactions and/or mate choice include size, bright coloration, ornamentation, weaponry and behaviors. In terms of intraspecific visual signaling coloration, size, and shape can be viewed as a compromise between the needs to attain mates and avoid being eaten. For example, the bright and bold upper wings of many male butterflies are exposed in flight and used in intraspecific signaling while the under wings, exposed when resting and feeding, are cryptically colored to avoid predation. Such visual compromises are common in some of our most glamorous butterfly species. They are sources of intraspecific genetic diversity and are of great interest to researchers and collectors.

Sexual dimorphisms in coloration in butterflies are a common result from the interplay of sexual selection and predation pressures. Females are relatively inconspicuous while the brightly colored males risk increased predation for increased reproductive success. Because males generally show the most dramatic coloration, and the taking of males is generally thought to have no effect on future population numbers, potential threats by collectors or predators can be lessened or negated by such adaptations. However, in female-limited mimicry complexes in which females, but not males, mimic other brightly colored, chemically protected species, it may be that females stand out and are particularly sought after.

The Influence of Apparency and Beauty in Valuation of Insects in Conservation

Economic, ethical, ecological, educational, and practical values attributed to particular species are used to prioritize conservation efforts (for reviews see IUCN 1983, Morris et al. 1991, New 1995, Pyle et al. 1981, Samways 1994). Insect apparency and beauty impact how we value insects in all of these areas.

Insects are generally little valued economically (IUCN 1983). Small size and the associated lack of information contribute to this situation (Samways 1994). While some species are used as sources of products, medicines, and biological control, only a very few taxa are commercially valuable because of their apparency. These are typically traded as dead stock. Worldwide, dead stock trade of insects is valued at tens of millions of dollars annually (Morris et al. 1991). Single specimens of birdwings have been advertised for up to US $7000 (Morris et al. 1991). An unexplored way that aposematic insects might be commercially valuable is through their co-evolved chemical systems with plants. Because insect conspicuousness can serve as a flag for novel plant chemistry, such insects might be used as probes to survey for medicines or other useful bio-chemicals (Kremen et al. 1993).

Ethical arguments for insect conservation that are based on intrinsic values of individuals are philosophical extrapolations of human-based morality (Lockwood 1987). Such an ethical framework cannot favor individuals of undescribed species nor individuals of endangered versus common species (Samways 1994). Individual-based moral consideration is effectively apparency-biased because only insects that are obvious to humans gain support on such grounds (New 1995). Furthermore, aesthetically-valued taxa are more likely to gain support, especially when economic, cultural, ecological or practical values conflict with moral consideration (Samways 1990). Ethical considerations are practically without application in undeveloped countries and are often incongruent with community or landscape level conservation strategies. However, by focusing on the interdependence of the genome and the individual, conflicts between ethical and biological justifications of insect conservation are often reconciled (Samways 1994). The above arguments do not negate the importance of moral consideration of individuals of all species. Such consideration is commendably the basis of insect collection ethical codes.

Insects are by far most valued in conservation for their ecological roles. They are key components in the composition, structure and function of ecosystems (Hafernik 1992, Ricklefs et al. 1984, Wilson 1987). Insects are abundant herbivores and detritivores influencing directly and indirectly elemental cycling and net primary productivity (Seastedt & Crossley 1984). Ecological importance and beauty only rarely coincide. The human bias in favor of the apparent and beautiful may be particularly shortsighted in this regard.

Charismatic species can be successfully used in the communication of issues, needs, knowledge, and the benefits of insect conservation (Salwasser 1991). Environmental educational objectives in which glamorous insect species are particularly useful include the study of diversity, abundance and biomass, complexity, species radiation, history, biological and economic importance, and interaction with plants (Robinson 1991, in New 1995). Conservation studies that demonstrate population declines of glamorous species, especially butterflies, have increased the general public's awareness of the need to protect insects and their habitats (Hafernik 1992, Samways 1989, Thomas 1984).

Amateur involvement in conservation efforts, such as the Fourth of July Butterfly Count (Swengel 1990) and the Entomological Society of Victoria Butterfly Mapping Scheme (New 1990(92)) are generally limited to well-appreciated, large, easily assessed taxa. Zoo and museum displays use almost exclusively large, apparent, and attractive species. Butterfly gardening has become a popular hobby and is promoted as a means to effectively demonstrate important ecological principles using mostly large, attractive species. It is common for naive butterfly gardeners to want to discourage unattractive larval stages that devastate their store-bought plants. However, the association of the less conspicuous, and usually less attractive, larvae with the appreciated, sought after adults teaches the need for the less-than-beautiful and the need to provide habitat. Experienced gardeners usually come to appreciate larval forms and behaviors.

Large, conspicuous insects offer unparalleled opportunities for conservation-related research. Unlike their vertebrate counterparts, they are accessible, easily reared, short lived, diverse, and inexpensive to study. Theoretical studies of apparent species provide important models for developing conservation methodology and setting conservation priorities that are unique to invertebrates (e.g. Hanski & Thomas 1994, Ehrlich & Murphy 1987, Murphy et al. 1990, Murphy & Weiss 1988).

Anthropogenic Threats to Insects, and Vulnerabilities of Large, Apparent Insects

Public support for conservation continues to rest on emotional rather than intellectual motives, and has been garnered primarily by the cute and cuddly vertebrates. Most adults dislike or are afraid of arthropods. This reflects our biased awareness of almost exclusively injurious insects (Byrne et al. 1984, Kellert 1993). Modern agriculture, and the usual resulting information bias toward small, unattractive, harmful pests, is largely responsible for such negative public perceptions (Barnes 1985). Innate fears may also contribute to human biases against insect conservation, especially when species are inconspicuous, unattractive, and economically unimportant (Kellert 1993). Such fears may be especially well-ingrained by certain aposematic insects. On the other hand, it is also the bright, big and bold insects, especially beneficial ones, that can be used most effectively to overcome ignorance, prejudice, innate fears, and anthropocentric biases against the small and often ugly world of insects (Morris 1987, Samways 1992).

Insects face the same anthropogenic threats as vertebrates, including changes to their habitat, impacts by exotics, pollution, climate change, pesticides, and, potentially, their collection for profit. The most important threat is habitat loss, fragmentation, and/or degradation. Unlike that seen in vertebrates, there is no general positive relation between insect size and their vulnerability to extinction (Samways 1994). This suggests that, although large, conspicuous species may sometimes face increased vulnerabilities due to their associated ecological needs, the conservation focus on large, conspicuous species is not biologically sound in general.

Climate change potentially affects insects both directly and indirectly through plant associations (Dennis 1993, New 1995). Apparency-related aspects of butterfly biology have led to their use as models for understanding the direct impacts of atmospheric pollutants and for predicting the indirect effects of climate change. For the same reasons, butterflies are promoted as monitors of climate change (Dennis 1993).

Pesticides have been blamed for insect species extinctions, but there have been no documented cases of such extinctions (IUCN 1983, Pyle et al. 1981, Thomas 1984). This is not to say that pesticides have not or can not lead to insect extinctions under certain circumstances. Furthermore, pesticides may influence insect community structure by changing the distribution and relative abundance of species (Samways 1994).

After habitat destruction, the negative impacts of non-indigenous species is considered the greatest threat to insect conservation. Including all known animal taxa, by far, most documented non-indigenous species in the US are accidentally introduced insects. Their impact is assumed to come primarily through interspecific competition and increased predation pressures (US Congress, Office of Technology Assessment 1993). However, the impacts of these non-indigenous species are rarely documented, except for economically important or charismatic species, because insects are generally unapparent, unappreciated, and, therefore, neglected in conservation.

Size also influences our knowledge of the environmental risks posed by biological control organisms. For example, microorganisms are thought to offer the greatest potential in biological control. However, due to their great diversity, minute size, and inaccessibility, we know almost nothing about their biology and ecology (Pimentel 1980). Classical biological control agents, such as nematodes, fungi, protozoa, bacteria, and viruses may have host ranges beyond their targeted species (Pimentel 1980, Samways 1988). However, their potential impact is rarely studied. When impacts are assessed, they are judged by aesthetically pleasing or economically valued species. For example, *Bacillus thuringiensis* has been shown to negatively affect more than 135 non-target species (Laird 1978, in Pimentel 1980), but it has generally received positive reviews because it has not been documented to be harmful to the natural enemies of economically important pest species. *Bacillus thuringiensis israelensis*, used in mosquito control, has received conservation attention because it has been shown to cause mortality in mayfly and dragonfly larvae (Zgomba, Petrovic & Srdic 1986, in Samways 1994). The general lack of conflict of interest between insect conservation and classical biological control lies partly in the fact that biological control is most often aimed at small, inconspicuous, unpopular, exotic species, while conservation efforts are aimed at large, conspicuous, popular, rare, and, often, specialized species (Samways 1988). The general absence of public demand for more strict pre- and post-release assessments of imported exotic biological control agents is related to the fact that obvious, charismatic species have rarely been noticeably impacted. *Bacillus thuringiensis,* released for gypsy moth control, may raise public concern if butterflies, even non-indigenous species, are found to be negatively impacted as suspected (Harbrecht 1991).

Insect collection for trade, commodity production and research is biased toward large, apparent species due to their aesthetic value and practical advantages. Taxa that are valued by collectors may benefit through the associated increased knowledge that is necessary for most species-oriented conservation efforts. Live trade of insects is highly biased toward large, aesthetically pleasing species but these are often bred from very few wild-caught animals. Butterfly farming and ranching are considered viable sustainable use strategies in which very high demand species are reared or encouraged to breed by providing them with host plants in their natural environment. A subset of these are then collected and used for economic gain, while the remaining are left to maintain or even boost natural populations.

The potential impact of collectors on insect populations remains a hotly debated topic, especially among lepidopterists. For recent controversial opinions, see *The News of the Lepidopterists' Society* (38 (1-2) 1996). The consensus appears to be that collectors rarely, if ever, are the primary cause of insect population or species extinctions (IUCN 1983, Morris 1987, New 1995, Orsak 1978(81), Pyle et al. 1981, Samways 1994, Thomas 1984). However, the scientific study of the impact of collection on vulnerable species is lacking. Insect collection is considered an ethical issue, but only specialist trade of wild-caught specimens, where value is heightened by rarity, is considered potentially threatening to populations. These rare species are often K-selected. Low reproductive rates, limited ranges and very specific host plant associations can increase vulnerability to collection and the habitat destruction that can be associated with economic gain. *Parnassius apollo* and New Guinea birdwings are examples of K-selected insects that are apparently threatened by collecting (Pyle 1978(81)).

INSECT APPARENCY AND CONSERVATION POLICY

Insect conservation policy primarily addresses the protection of rare species, with provisions for those species' habitats, and/or general restrictions on insect collection. Such policies are extensions of vertebrate-based conservation philosophies and are generally not objective nor consistent (New 1995). This is partly due to logistical constraints related to the small size and inconspicuousness of most insect taxa. It is easier to assess population status, develop management plans, and monitor large, conspicuous species. Their conservation need is more likely to be demonstrated by pre-existing data necessary to document population decline. Their study is more likely to secure funding and public support.

Just as with vertebrates, charismatic insect species are sometimes intentionally given conservation priority for political reasons. In Britain, the Swallowtail, *Papilio machaon*, was included in the Wildlife and Countryside Act (1981) as a political ploy. Its inclusion was based on glamour status and historical focus and was contrary to scientific data that indicated a low priority in conservation need (Morris 1987). Furthermore, charismatic species that are not considered a high conservation priority may be listed because their preservation is expected to serve as an umbrella for other species. Such an umbrella can be quite effective. Habitat protection for the El Segundo blue, *Euphilotes bernardino allyni*, has helped to protect 15 other less-glamorous invertebrate species that co-inhabit the preserved California sand dune ecosystem (Mattoni 1992).

The US Endangered Species Act (ESA) of 1973 is considered the most powerful conservation policy in the world. Although the ESA theoretically gives equal status to all species, in practice charismatic species are strongly favored. Fewer than 10% of listed species received more than 90% of the funding in 1990, and none of these is an insect (New 1994)! ALL insects receive little attention relative to their representativeness in species diversity or their ecological importance. Small size, lack of aesthetic appeal, and associated lack of knowledge, support, and funding further bias listing efforts within the Insecta (Boecklen 1987, Hafernik 1992, Murphy 1991, Van Hook 1994). As of 1989, 95% of the 427 insect species assessed for listing were not listed due to insufficient information (Opler 1991). There have been 28 insects put on the list of endangered and threatened wildlife, 19 of which are butterflies. Recovery plans exist for only four species, all of which are butterflies (Opler 1995).

The ESA is an example of the wrong approach at the wrong scale (*sensu* Murphy 1989). The policy is criticized for lack of scientific bases, ineffectiveness and inconsistent use (Mann & Plummer 1992, Murphy 1991, Noss 1991, Rohlf 1990, Salwasser 1991, Scott et al. 1987, Tangley 1984, Wilcove 1992). All of these err in disfavor of insect conservation, and especially the less charismatic taxa. For example, vague terms like endangered and threatened have no consistent biological meaning. What constitutes a species is debatable, especially in plants and invertebrates. The use of such vague terminology creates both intended and unintended biases in conservation efforts and apparent species are often favored (Rohlf 1991). Below-species-level knowledge and conservation consideration are very rare in insects and restricted to glamorous taxa (Wilcove et al. 1992).

ESA biases in species listing that are related to apparency and appeal include 1) information is related to charisma, 2) species that are less charismatic are slower to be listed, even when data is available, 3) once listed, more attention and funding are directed toward charismatic species, and 4) small, inconspicuous species are difficult to survey (Tangley 1984). Once filtered through these biases, listed species are those thought to be especially threatened by anthropogenic impacts. Ecological specializations associated with, but not limited to, large, apparent species can increase these vulnerabilities (Murphy 1991).

Apparency-related biases in listing are also characteristic of state agency insect conservation policies. For example, the Technical Advisory Committee on Endangered Species for the Florida Committee on Rare and Endangered Plants and Animals is constrained in its efforts to identify rare species and develop recovery plans by apparency-related problems. These include small size, diversity of types, seasonality of form, lack of information and taxonomic problems (Weems 1977). Listed species are not necessarily the most worthy. They reflect the interests of taxonomic specialists and amateurs who provide the historical knowledge base needed to demonstrate population declines.

International conservation policies also generally favor charismatic species. For example, the criteria for nomination for the listing on the Berne convention (the Conservation of European Wildlife and Natural Habitats, 1979) includes a provision that the species must be easy to identify. Minute, inconspicuous insects, have undeveloped taxonomies, even in relatively well-studied areas like Europe, preventing listing of the major chunk of insect biological diversity. The International Union for the Conservation of Nature and Natural Resources (IUCN) Red Data Book is intentionally biased toward some glamorous groups, like butterflies and dragonflies, due to their high profile related to size, coloration, ease of identifying, and taxonomist specialization (Samways 1994). The aim is for these taxa to serve are umbrella species for the lesser endowed, less conspicuous species (Pyle 1978(81)). This bias is exemplified in the Sweden Red Data Preliminary List (1987) which includes 786 species, of which over 300 are Coleoptera and over 250 are Lepidoptera. This predominance reflects the high diversity of these groups, but also reflects their relatively greater number of large, conspicuous species compared to other groups. The Convention of International Trade in

Endangered Species of Wild Fauna and Flora (CITES) of 1973, an international agreement aimed at protecting rare species from economic abuses through trade, lists 10 insect species. All of these are lepidopterans (New 1995). The Bonn Convention on the conservation of migratory species of wild animals (1979) lists only the charismatic monarch butterfly.

As noted above, overcollection is rarely considered to threaten insect populations. Furthermore, there is no evidence that restrictions on collection benefit insect population numbers (Hama et al. 1989, in Sibatani 1990(92)). Inconsistent with this knowledge, most insect conservation policy consists only of restrictions on collectors or insect trade (Pyle et al. 1981). When broader-based policies exist, collection and trade restrictions are usually retained (e.g. ESA). This is a carry over of vertebrate-based evidence that population declines result from overexploitation. We need scientific consensus on if, when, where, and how collection impacts insect populations if we are to develop more appropriate insect conservation policy.

Biases in our perception and appreciation of insects contribute to the problems of policy restrictions on insect collection. These include 1) broad restrictions are often without biological rationale and may unduly restrict amateur interest, 2) restrictions are often biased in enforcement, 3) policy often does not reflect species need, but aesthetic appeal and the associated higher levels of knowledge, 4) bureaucratic, and enforcement costs may compete with habitat protection, 5) insect surveys necessary to document population declines are severely restricted, and 6) restrictions can increase exploitation when the perceived rarity is related to value (New 1995).

All insect collection is prohibited without a permit in most protected areas in many, especially developed, countries. These restrictions are meant to serve as umbrella protection measures, but such policies lack scientific bases and unduly inhibit the gathering of information and the development of amateur interest (Morris 1987, New 1990(92), Samways 1994, Sibatani 1990(92), and Thomas 1984). For example, in an effort to protect one species, the satyrid (*Erebia christi*), in some areas of Switzerland it is illegal to carry a butterfly net (New 1995). At the other extreme, The Indian Wildlife Protection Act lists approximately 450 butterfly taxa as protected and prohibits specifically the collection of these species (New 1995). The identification problems associated with small size and inter- and intraspecific phenotypic variation make such policies practically self-defeating.

All-inclusive collection restrictions are rarely enforced due to the necessary costs and bureaucracy. However, recently, the US Fish and Wildlife Service has brought several collectors to court over the taking of insect specimens without a permit on protected lands. Sporadic, inconsistent enforcement is biased in time and in space, is restricted primarily to charismatic taxa such as butterflies, and has estranged amateur collectors (for recent accounts of this controversy see *News of the Lepidopterists' Society* 38 (1-2) 1996).

When collection restrictions are less than all-inclusive, they are focused toward charismatic taxa. Such restrictions assume collection can negatively impact insect populations in general and then use collector interest to direct restrictions. This is a conservative approach that results from a lack of information. Under the British Wildlife countryside act of 1981, it is illegal to kill, take, or sell 14 insects (Drewett 1988), all of which are relatively conspicuous species. The Federal Republic of Germany prohibits collection of large lepidopterans (Morris 1987). In some European countries all butterflies are protected from collection. Interestingly, the pestiferous white pierids are exempted from such restrictions (Collins 1987, in New 1995).

In Germany, all Odonata are protected from collection, while the impact of acid rain in their conservation is largely ignored (Samways 1994). In Japan, protection legislation is limited almost exclusively to collection prohibitions for butterflies, thought to be of little or no benefit, while preservation of insect habitats is ignored (Sibatani 1990(92)).

Many conservation, amateur, and scientific organizations have published voluntary insect collection codes. These often cover all species, but are aimed at glamorous, not necessarily rare, species. These restrictions are based on ethical rather than biological grounds. They rightly discourage collection of very rare species, over-collection of any species, and wasteful collection methods.

Insect Apparency and Practical Implications for Conservation

Practical problems with both species and larger-scale approaches to conservation that are related to apparency and appreciation of insects include 1) the paucity and complexity of taxonomic and ecological knowledge, 2) monitoring problems, and 3) biases in research, funding, amateur interest, and public support (New 1995).

There is approximately one taxonomist for every 425 described insect species (Samways 1994). This ratio creates a taxonomic impediment that becomes even more daunting when we consider that fewer than 5% of existing insect species are thought to be described (Raven 1990). The taxonomic limitations arising from the practical difficulties of observing and studying very small organisms is so great that microorganisms must be classified functionally rather than morphologically (Chapin et al. 1992). Funding and expertise interest are biased toward aesthetically appealing and economically important species, and both are most lacking in undeveloped, tropical areas where insect species diversity is highest.

Apparency differences associated with life stage, microhabitat, sex, and season are not appreciated by traditional taxonomic methods but are critical to ecologically-oriented conservation efforts (Samways 1994). Phenotypic variation, such as color polymorphisms, cryptic species, and sibling species, also confuse species-status determination. It is difficult to accurately assess the population status, develop management plans, or monitor such ambiguous groups. The use of dead specimens further compounds the problem of taxonomic designation. For example, the satyrid butterfly, *Oeneis bore*, has two color forms that behave as separate species in the field but is treated as one species using phenotypic techniques that rely on dead specimens (Ferris 1986). Naturalists studying live animals in their natural habitats and molecular systematic methods are necessary to overcome some of the shortcomings of traditional taxonomic methods. Both practical and theoretical problems with species status designation have not been adequately confronted in species-level conservation approaches. Community- and landscape-level conservation strategies overcome some of these taxonomic-related problems but these approaches also rely heavily on species classification.

The extreme diversity, small size, inconspicuous habits, and the taxonomic and ecological ignorance associated with these aspects of insect biology prevent species-by-species inventorying. New (1995) suggests three strategies aimed at getting around this problem: 1) the use of indicator groups, 2) taxonomic reduction, and 3) the use of ecologically functional groups. Taxonomic reduction includes grouping by higher than species level taxa and grouping by morphological characters or recognizable taxonomic units. Both taxonomic reduction and the use of functional groups rely on apparency-related adaptations to alleviate other apparency-related obstacles in insect conservation. For example, size, coloration, and morphological structures related to feeding strategies are used to group species with similar ecological function.

The assessment of potential impacts of climate change, pesticides, non-indigenous species, and collection on insect populations is primarily restricted to aesthetically pleasing and economically important species. This reflects interest, knowledge and monitoring methodologies that are beauty- or necessity-biased. The potential impacts of pesticides are little-studied for any non-target species. To date, monitoring the impacts of non-indigenous species, including biological control agents, is almost exclusively restricted to economically important or glamorous species (Ehler 1991). It is expected that further studies will confirm the environmental safety of most classical biological control agents (Samways 1988). However, the potential environmental dangers of releasing irretrievable, mobile, evolving organisms and our paucity of data on the impacts of these non-indigenous species on their new environment are forming a barricade to the development of this important pest-control strategy (Samways 1994). Most attempts to document potential negative impacts of collecting on insect populations come from studies on attractive taxa, almost exclusively butterflies. This is appropriate since they are particularly sought after, but the documented impacts or lack thereof may not be representative of such a diverse group as the Insecta.

Problems Associated with Single Species Approaches to Insect Conservation

Species listing and the development of recovery plans are very demanding in terms of both historical and ecological information and financial and public support. We can afford these costs only for relatively glamorous species and only in relatively wealthy nations. For example, in the IUCN Invertebrate Red Data Book (1983), all examples of anthropogenic impacts on insects resulting from changes in land, water, pollution, loss of associated species, and importation of exotics were documented for large, apparent species in developed countries. Only water-pollution impacts were noted for inconspicuous species, probably reflecting a long history of using invertebrates as environmental indicators of water quality (Kremen et al. 1993).

Under the ESA, conservation priorities are based on biological uniqueness, degree of threat, and opportunity for success (Mann & Plummer 1992). Each of these is highly biased in favor of apparent and appreciated species for practical and emotional reasons. Most conservation efforts have been aimed at butterflies because they are obvious, enjoy high amateur interest, are easy to see and study, and are both harmless to humans and beneficial as pollinators. These aspects of butterfly biology make determination of uniqueness and threat easier to identify and also incite public support necessary to monitor and manage insect populations. In contrast, inconspicuous and unattractive parasites are generally ignored in conservation, even though they are considered extremely diverse and of conservation concern due to their generally extreme, obligatory specializations (Windsor 1995). Parasites are often only discovered when their hosts become extremely rare or extinct, and then they are often dismissed or even attacked in an effort to boost their host's survival (Windsor 1995). The demise of the Passenger Pigeon stands as one of the most exemplary, best-appreciated species losses. The simultaneous loss of its lice parasite has gone unnoticed and without concern (Stork & Lyal 1993, in Windsor 1995).

Species-oriented management plans are restricted almost exclusively to butterflies. The European Large Copper butterfly, *Lycaena dispar batava,* has been augmented since the 1930s, and this effort is expected to remain necessary for its continued survival in the wild (New 1995). Such costly efforts are not feasible for even the most well-studied and well-appreciated species in developed countries. They are likely to be counter-productive in understudied, speciose areas such as the tropics.

As with vertebrates, intensive management efforts, such as captive breeding, translocation and reintroduction programs, are initiated when species are at the brink of extinction with little chance of recovery. These risky and unpredictable tactics are costly in terms of funding, time, expertise, and research. They are restricted to charismatic or economically important species in developed countries. In Europe, 323 insect reintroductions or reinforcements have been attempted, with less than 60% established. All of these efforts were directed at butterflies (Oates & Warren 1990, in Samways 1994).

Recent releases of captive-bred Schaus Swallowtails (*Papilio aristodemus ponceanus*), an endangered subspecies under the ESA, demonstrate the sort of practical considerations that insect apparency forces on intensive management efforts. Researchers had to change from releasing cryptic pupae to adults because 65-99% of the pupae were lost to predation when placed in their natural habitat. Even in this relatively well-studied species, it is unknown how these rates compare to natural levels of predation, but it is thought that unnatural densities, positioning, and artificial pupation bases used in the releases may have voided the larvae's crypsis (Jaret Daniels, pers. comm.).

Variation in insect form and function related to seasonality, polymorphic types, sexual differences, and life stage specializations is an obstacle in species-oriented conservation strategies (Samways 1994). Such variation adds both confusion and time to the listing process and complexity to management plans, with apparent forms being favored. For example, critical habitat protection under the ESA includes areas outside the geographic area typically occupied, including hilltopping, hibernation, and aestivation areas. These are more likely to be known, and their preservation supported, for charismatic species.

Insect Apparency Biases and Implications for Large-Scale Conservation Strategies

It is not feasible or biologically rational to appraise insects species-by-species for conservation needs, due to their extreme diversity in species and ecological roles, and habitat requirements. More and more, single-species approaches are combined with ecosystem approaches to conservation. Larger-scale (than species) approaches rely on reducing the volume and complexity of information necessary to preserve and manage species and natural areas through innovative methods of assessment, management, and monitoring (Hunter 1991). These approaches rest on empirical knowledge, ecological theories, and model development that are in their infancy (Salwasser 1991). Large, brightly colored insects are most likely to contribute to each of these. They are also more likely to enjoy funding priority and expert attention.

Large-scale approaches in conservation relieve the need to prioritize conservation efforts by values associated with charisma. However, biases toward large, conspicuous species are retained for monitoring and assessing conservation sites. Five types of species are of paramount importance in ecosystem approaches to conservation. These include 1) species used as indicators of diversity or monitors of environmental change, 2) keystone species: those that play a critical role in the structure and function of an ecosystem, 3) umbrella species: those whose conservation serves to protect other species, 4) flagship species used as a focus for funding and generating support, and 5) species that are particularly vulnerable to extinction due to their biology and/or ecology (Noss 1991). The discovery and use of each of these types of species are apparency-biased due to disproportional levels of information and the prevailing anthropocentric conservation perspective.

Insects are increasingly used as indicators of biogeographic zones, areas of endemism, community richness, diversity, naturalness, typicalness, and centers of evolutionary radiation in conservation planning (see Kremen 1992, Kremen et al. 1993, and references therein). Favored groups are readily observed and collected, are well known taxonomically and ecologically, and are valued aesthetically and/or economically (Kremen et al. 1993). These biases are intended and often necessary. They may or may not be biologically legitimate. For example, dipteran and hymenopteran parasitoids are potentially good indicator species, due to their association with diverse ecological niches and microhabitats, widespread occurrence and correlated trends with other groups. However, Disney (1986b, in New 1995) showed that mapping the distributions of Diptera is limited due to practical shortcomings associated with their apparency. We must use the distribution and abundance of obvious, easily sampled species.

To better assess representativeness, uniqueness, and typicalness of areas in order to set conservation priorities, we need to develop more efficient sampling methods (New 1995). The use of parataxonomists or amateurs to help with the tremendous amount of sorting and identification necessary for conservation-related work is becoming increasing popular (but see Rosenberg et al. 1986). Such innovative approaches are necessary and effective, but accuracy is generally sacrificed for efficiency. Furthermore, the loss of accuracy is not consistent across taxa, but is apparency biased. For example, in a study of the performance of non-specialists in assessing samples of aquatic insects, Cranston and Hillman (1992) showed that increased variability was correlated with small body, increased number of closely related taxa, and morphological variability within species.

In management, insects are used to monitor human disturbance and ecological change, including changes in habitat, ecological disruption, climate change, and pollution. Insects are sometimes favored as monitors over vertebrates because they are particularly sensitive, respond rapidly, and offer a smaller-scale probe (e. g. Kremen et al. 1993, New 1995, Sparrow et al. 1994, Thomas & Mallorie 1985). They are also increasingly used to supplement vertebrate monitoring because of their unique habitat needs and responses to anthropogenic threats. Useful groups must be ecologically specialized and, due to the need for reproducible sampling methods and historical information, they are generally large, and apparent. Butterflies are preferred as indicator species and monitors of environmental change specifically because of their apparency and charisma (Samways 1994). They are specialized, well known taxonomically and ecologically, have established monitoring methods, and strong amateur interest and public support (Kremen 1992, Kremen et al. 1993, Thomas 1991).

Umbrella species are notable taxa that are characteristic of a particular habitat that, when preserved, benefit many unstudied, unappreciated species in the community. The value of a particular species to serve as a protective umbrella is based on ecological requirements, such as the need for large diverse habitats. However, the need for historical and ecological information, as well as public support, favors the designation of apparent and appealing species for this role (New 1994). The monarch butterfly is an example of an umbrella species. The focus of research, conservation attention, and public support for monarch conservation enhances the potential to preserve the remaining flora and fauna of the highly fragmented, isolated fir forest relics that constitute their threatened overwintering grounds in the highlands of Mexico.

DISCUSSION

Large, conspicuously colored insect taxa are given special attention in species-oriented conservation. This focus is both legitimate and intended. It is based on special threats and ecological needs associated with a species' apparency and on conservation values, public support and policy aims. However, the apparency bias is also a sometimes unintended, and sometimes unnoticed, bias, resulting from practical aspects of insect ecology and conservation methodology.

Empirical and theoretical contributions by entomologists are needed to improve existing species-focused conservation efforts, to better develop larger scale approaches, and to help build conservation policies that better reflect the unique conservation needs of insects. Particularly important is the need to develop generally applicable population models using representative insects, to develop better sampling methods, and to better integrate conservation and agriculture programs.

In species-oriented conservation efforts, ALL insects are relatively small and inconspicuous, and are highly disfavored in conservation efforts relative to their vertebrate co-inhabitants. This reflects the lack of ecological and taxonomic knowledge, research, funding, public and policy support, and sampling problems. These impediments point to the value of increasing large-scale conservation research, education, and policy directives. The use of insects as tools for assessing, managing and monitoring landscapes promotes ecosystem and regional approaches that are critical to all future conservation efforts. Large-scale conservation strategies also rely on both intended and unintended biases toward large, conspicuous insects. Entomologists can help to identify and lessen detrimental biases and document strengths through theoretical and empirical contributions.

The relatively recent focus on insects as targets and tools in conservation points to the need to broaden the discipline of entomology and to better bridge our work with amateurs, ecologists and conservation biologists. The study of pest and glamour species has much to offer conservationists. However, to achieve the broader goals of sustainability in agriculture and conservation, entomologists need to discard our own biases. We need to better address the 99% of species not generally considered in pest-oriented research (Wilson 1987). We cannot afford to cut our funding or attention to the development of innovative, ecologically sensible solutions to pest problems. However, we can no longer ignore the fact that sustainable agriculture rests on functioning natural ecosystems both near and far from the agricultural fields. These natural systems are insect-dominated, but by neither characteristically beautiful or pestiferous species. Their study is critical both to the future sustainability of agriculture and to agriculture's contribution to the conservation of biological diversity.

Effective and efficient conservation strategies cannot depend solely on public support for charismatic species that are emotionally valued. Although we can, and must, learn affinities for species that are unfamiliar to and different from ourselves, we most readily learn about, care about, and make sacrifices for species that are apparent, aesthetically appealing and demonstrate positive human benefits. Exposure to glamorous insects will help bridge the gap between our natural human affinity for the cute and cuddly and the needed appreciation of often non-intuitive ecological principles. Until we cross that bridge, we will continue to make irresponsible personal and social decisions. Increasing the ecological awareness of policy makers and the general public is the most important and timely conservation challenge. Entomologists study the most diverse, ubiquitous and, arguably, most important taxa in conservation. We are the best equipped to rid negative biases against insects and to instill an appreciation of the importance of insects to our sustainable future.

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