

Review Article

Preemptive Circular Defence of Immature Insects: Definition and Occurrences of Cycloalexy Revisited

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Cycloalexy was coined by Vasconcellos-Neto and Jolivet in 1988 and further defined by Jolivet and collaborators in 1990 in reference to a specific type of circular defence. The term has been applied to numerous organisms, including adult insects, nymphs, and even vertebrates, but has lost precision with the accumulation of anecdotal reports not addressing key elements of the behaviour as first defined. We review the literature and propose three criteria that are sufficient and necessary to define the behaviour: (1) individuals form a circle; (2) defensive attributes of the individuals are positioned on the periphery of the circle, and as a result, the periphery of the circle uniformly contains either heads or abdomens; (3) animals preemptively adopt the circle as a resting formation, meaning it is not necessary to observe predation. When these considerations are taken into account, cycloalexy appears less common in nature than the literature suggests. We argue that unequivocal cases of cycloalexy have been found only in sawflies (Tenthredinoidea: Pergidae, Argidae), leaf beetles (Chrysomelidae: Galerucinae, Cassidinae, Chrysomelinae, Criocerinae), weevils (Curculionidae: *Phelypera distigma*), and midges (Diptera: Ceratopogonidae, *Forcipomyia*). Reports of cycloalexy in caterpillars (Saturniidae: Hemileucinae: *Lonomia*, Papilionidae) require further documentation. We report one new case of cycloalexy in thrips (Thysanoptera) and question reports of cycloalexic behaviour in other taxa.

1. Introduction

Some animals show a remarkable behaviour: they group in a tight circle for defence [1]. This behaviour is reminiscent of Carl von Clausewitz's 1812 Principles of War: "In strategy (...) the side that is surrounded by the enemy is better off than the side which surrounds its opponent, especially with equal or even weaker forces" [2]. Many animal species employ this strategy. For example, among vertebrates, muskoxen (*Ovibos moschatus*, Blainville, 1816) form a circle enclosing the young calves when attacked by wolves, their principal natural predators [3, 4]. Their circular formation protects the most vulnerable body parts while the extremity that is best defended or involved in attack is at the periphery. Vasconcellos-Neto and Jolivet [5] coined the term "cycloalexy (kuklos = circle, alexo = defend)" to describe a particular behaviour of gregarious insect larvae. They defined their

new term as "the attitude adopted at rest by some insect larvae, both diurnal and nocturnal, in a tight circle where either the heads or ends of the abdomen are juxtaposed at the periphery, with the remaining larvae at the center of the circle. Coordinated movements such as the adoption of threatening attitudes, regurgitation, and biting, are used to repel predators or parasitoids." [1]. Several elements of the original definition distinguish cycloalexy from other circular formations occurring in nature.

However, as new examples of the behaviour have been proposed in the literature without addressing key aspects of the original definition, the distinctions between cycloalexic behaviour and other circular formations have become imprecise and weakened the concept of cycloalexy. Here, we will review reported examples of cycloalexy and question whether they meet the criteria of a revised definition or are alternative forms of aggregation. Our revised definition

strives to adhere to the key aspects of cycloaexy as originally defined, while removing arbitrary and unnecessary criteria. This way, cycloaexy can be recognized as an evolutionarily convergent behaviour rather than several superficially similar behaviours.

1.1. Redefining Cycloaexy. The defensive nature of cycloaexy is paramount as it is found in the etymology of the term: “to defend” [11]. However, this key aspect of the behaviour can be problematic since cycloaexy has often been invoked upon fragmentary observations of groups rather than controlled ecological studies. Nevertheless, until species can be more thoroughly studied, we suggest that three criteria are sufficient to distinguish cycloaexy from other behaviours.

Criterion 1: Individuals Are Arranged in a Circle. The original definition specified “in a tight circle” [1], but we argue that tightness is subjective and should be removed from the definition.

Criterion 2: The Extremity Bearing Defensive Attribute Is Positioned Outwards. In the original definition, the periphery of the circle is uniform: “either the heads or ends of the abdomen are juxtaposed at the periphery” [1], sometimes with individuals at the centre with neither head nor abdomen reaching the periphery. This means that peripheral individuals in a given group face outwards or inwards, but not both. We argue that, in this statement, it was implicit that the best defended extremity is at the periphery since it is unlikely that individuals with their vulnerable side out could ever be at an advantage. Uniformity of the circle in this respect, then, becomes a corollary of our second criterion.

Criterion 3: The Circle Is Adopted as a Resting Formation. Following the original definition, we limit cycloaexy to cases when individuals are in resting or quiescent, nonfeeding periods. This makes cycloaexy a preemptive behaviour.

These criteria allow for the initial identification of cycloaexy by rapid, visual assessment. If later studies disprove defensiveness, then the behaviour studied is not cycloaexy. Additionally, although not specified in the original definition, we suggest adding the distinction that the behaviour is for the defence of the individuals themselves and others within the group, as opposed to the defence of a resource or nest. We also suggest removing the criterion that “Coordinated movements such as the adoption of threatening attitudes, regurgitation, and biting, are used to repel predators or parasitoids” [1], for several reasons. Cycloaexy is notably preemptive, taken regardless of the immediate presence of a threat; in some species, immature animals have passive defences made more efficient by a circular formation; and the second criterion of our amended definition already includes defence, either passive or active. Finally, although the original definition was limited to insect larvae, in this paper, we review all reports of cycloaexy and suggest removing the limitation altogether.

2. Results

See Table 1.

3. Discussion

3.1. Strict Cycloaexy. Among the records in the literature, some species demonstrate behaviour that precisely fit the revised definition and our three essential criteria of cycloaexy (Table 1). This is the case of *Coelomera* spp. (Coleoptera: Chrysomelidae: Galerucinae) and spittfire grubs *Perga dorsalis* Leach, 1817 (Hymenoptera: Tenthredinoidea: Pergidae) [1].

Approximately 35 species of genus *Coelomera* are cycloaexic and feed on *Cecropia* (Urticaceae). Most *Cecropia* plants are myrmecophytes protected by mutualistic *Azteca* ants (Formicidae: Dolichoderinae). The gregarious leaf beetle larvae feed during the day and rest at night, in a tight circular cluster with heads inside and abdomens at the periphery [7, 8]. Their rear end is protected by a supra-anal shield and, when threatened, these larvae excrete a nauseating fluid from the anus. Therefore, the better protected part of the insect, the posterior, is facing outwards in the circle, with the more vulnerable head inside [7, 8]. Thus, by orienting the same way, individual larvae protect themselves and other members of the group (Figures 1 and 2).

Spittfire grubs *Perga dorsalis* feed on *Eucalyptus* during the night and rest during the day in a circular formation [47]. The larvae rest with their heads at the periphery of the circle, with some larvae in the middle of the aggregation. When threatened, the larvae rear their heads and abdomens and regurgitate oils sequestered from their host *Eucalyptus* [47]. The oils are an effective deterrent of potential predators, including ants, birds, and mice [49]. The heads are the better protected part of the insects and, again, form the periphery of the circle.

3.2. Examples of Cycloaexy That Do Not Agree with the Revised Definition

3.2.1. The Oxymoron of Noncircular Cycloaexy. Gregarious caterpillars of genus *Arsenura* (Saturniidae: Arsenurinae) are reported to “show a kind of cycloaexy when resting on tree trunks during the day” [1]. The caterpillars align side-by-side or head-to-abdomen or both, in an elongated oval cluster [11]. The posture of these caterpillars with their heads, sides, and abdomens at the periphery in a linear mass rather than a circle does not meet the first criterion of the revised definition of cycloaexy. The circle formation with the best defended extremity outwards is an important characteristic of cycloaexic behaviour. *Arsenura* are gregarious and rest in a tightly aggregated mass, but they are not cycloaexic. Santiago-Blay et al. [11] suggest that, on a tree trunk, “the available background surface makes the shape of the larval aggregation distorted.” However, on the scale of a caterpillar, and depending on the diameter of the tree, a tree trunk can be quite large and nearly flat. In addition, probable cycloaexy on tree trunks has been observed in *Lonomia* sp. (Figure 3(b)). We suggest the caterpillar aggregations described by Santiago-Blay et al. [11] are less circular and compact not because of the shape of tree trunks but because *Arsenura* caterpillars’ resting positions are not cycloaexic.

TABLE 1: Reported cases of cycloaexy and how they fit within the revised definition.

Organism	1 Circular formation	Criteria 2 Best defended extremity at the periphery	3 Default rest position	Aggregation is defensive (not for nest protection)	Is the behaviour cycloaexy?	Reference
Coleoptera: Chrysomelidae:						
Galerucinae						
<i>Coelomera</i> spp.; for example, <i>C. ruficornis</i> Baly, 1865; <i>C. helena</i> Jolivet, 1987; <i>C. raquia</i> Bechyně, 1956; and so forth	Yes	Yes, abdomens	Yes	Yes	Yes	[1, 5–8]
<i>Dircema</i> spp.	Not observed	Not observed	Not observed	Not observed	None observed	[6, 7]
Coleoptera: Chrysomelidae: Criocerinae						
<i>Lema</i> sp.;						
<i>Lema apicalis</i> Lacordaire, 1845 and <i>L. reticulosa</i> Clark, 1866	Yes	Yes, heads	Yes	Yes	Yes	(Figure 1(a)) [9, 10]
<i>Liliocerus nigropectoralis</i> (Pic, 1928), <i>L. formosana</i> Heinze, 1943	Yes	Yes, heads	Yes	Yes	Yes	(Figure 1(b)) [11]
Coleoptera: Chrysomelidae: Chrysomelinae						
<i>Agrosteomela chinensis</i> (Weise, 1922)	Not observed	Not observed	Not observed	Not observed	None observed	[11–13]
<i>Chrysophtharta obovata</i> (Chapuis, 1877)	Yes	Yes, abdomens	Yes	Probably	Yes	[11, 14]
<i>Doryphora paykulli</i> (Stål, 1859), <i>D.</i> <i>reticulata</i> Fabricius, 1787	Yes	Unclear, abdomens	Yes	Yes	No*	[15]
<i>Eugonycha melanostoma</i> (Stål, 1859)	Yes	Unclear, abdomens	Not reported	Not reported	Tentatively	[7, 11]
<i>Gonioctena sibirica</i> Kimoto, 1994	Roughly	Unclear, mostly abdomens	Mostly	Unclear	Unclear	[11, 12, 16]
<i>Labidomera suturella</i> Guérin-Méneville, 1838	Not observed	Not observed	Not observed	Not observed	None observed	[11, 17–19]
<i>Paropsis</i> spp.; for example, <i>P. aegrota</i> Boisduval, 1835, <i>P. maculata</i> (Marsham, 1908), <i>P. atomaria</i> Olivier, 1807 and <i>P. tasmanica</i> Baly, 1864	Not circular	No, mixed extremities	No	Perhaps, unclear	No	[7, 11, 14, 20, 21]
<i>Paropsisterna</i> spp.	Not reported	Not reported	Not reported	Not reported	Not enough information	[11, 12, 14, 20]
<i>Plagiodera</i> spp. for example, <i>P. versicolora</i> (Laicharting, 1781)	Not circular	No, mixed extremities	No	No	No	[7, 22–25]
<i>Phratora</i> spp.	Not observed	Not observed	Not observed	Not observed	None observed	[7, 11]
<i>Phyllocharris undulata</i> (Linnaeus, 1763)	Roughly	Unclear, mostly abdomens	No	Not observed	No	[11, 26]
<i>Platyphora selva</i> Daccordi, 1993, <i>P. microspina</i> (Bechyně, 1954)	Yes	Unclear, abdomens	Yes	Yes	No*	[15, 27]
<i>Platyphora conviva</i> (Stål, 1858), <i>P. anastomozans</i> (Perty, 1832), <i>P. nigronotata</i> (Stål, 1857), <i>P. nitidissima</i> (Stål, 1857)	Yes	Yes, heads	Yes	Yes	Yes	[7, 9, 10, 28]
<i>P. fasciatomaculata</i> (Stål, 1857), <i>P. vinula</i> (Stål, 1858)						

TABLE 1: Continued.

Organism	1 Circular formation	Criteria 2 Best defended extremity at the periphery	3 Default rest position	Aggregation is defensive (not for nest protection)	Is the behaviour cycloaexy?	Reference
<i>Proseicela vittata</i> (Fabricius, 1781), <i>P. bicrucata</i> Jacoby, 1880, <i>P. spectabilis</i> (Baly, 1858)	Yes	Unclear, abdomens	Yes	Yes	No*	(Figure 5(a)) [15]
<i>Proseicela crucigera</i> (Sahlberg, 1823)	Yes	Unclear, abdomens	Yes	Yes	Not enough information	[7, 9]
<i>Pterodunga mirabile</i> Daccordi, 2000	Yes	Unclear, abdomens	Not reported	Not reported	Not enough information	[11, 12, 19]
Coleoptera: Chrysomelidae: Cassidinae						
<i>Acromis sparsa</i> (Boheman, 1854)	Yes	Yes, abdomens	Yes	Yes	Yes*	[7, 11, 29]
<i>Aspidomorpha puncticosta</i> Boheman, 1854,	Yes	Yes, abdomens	Yes	Yes	Yes	[7, 30–32]
<i>A. miliaris</i> (Fabricius, 1775)						
<i>Chelymorpha informis</i> Boheman, 1854, <i>C. alternans</i> Boheman, 1854, <i>C. cribraria</i> (Fabricius, 1875)	Yes	Yes, abdomens	Yes	Yes	Yes	[7, 8]
<i>Cistudinella foveolata</i> (Champion, 1894)	Yes	Yes, abdomens	Yes	Probably	Yes	(Figure 2(a))
<i>Conchyloctenia punctata</i> (Fabricius, 1787)	Yes	Yes, abdomens	Yes	Yes	Yes	[7, 30, 33]
<i>Coptocycla dolosa</i> Boheman, 1855	Yes	Yes, abdomens	Yes	Probably	Yes	(Figure 4)
<i>Eugenysa columbiana</i> (Boheman, 1850), <i>E. coscaroni</i> Viana, 1968	Yes	Yes, abdomens	Yes	Yes	Yes*	(Figure 2(b)) [34, 35]
<i>Paraselenis flava</i> (Linnaeus, 1758)	Yes	Yes, abdomens	Yes	Yes	Yes*	[8]
<i>Nuzonia</i> sp.	Yes	Yes, abdomens	Yes	Yes	Yes	(Figure 2(c))
<i>Ogdoecosta biannularis</i> (Boheman, 1854)	Yes	Yes, abdomens	Yes	Yes	Yes	[7, 11, 36]
<i>Omaspides tricolorata</i> (Boheman, 1854), <i>O. pallidipennis</i> (Boheman, 1854), <i>O. sobrina</i> (Boheman, 1854), <i>O. bistrata</i> (Boheman, 1854) and <i>O. convexicollis</i> Spaeth, 1909	Yes	Yes, abdomens	Yes	Yes	Yes*	[7, 11, 32, 35, 37–39] (D. Windsor's observations)
<i>Physonota alutacea</i> Boheman, 1854	Yes	Yes, abdomens	Yes	Probably	Yes	(Figure 2(d))
<i>Polychalma multicava</i> (Latreille, 1821)	Yes	Yes, abdomens	Yes	Probably	Yes	(Figure 2(e))
<i>Stolas</i> sp., <i>Stolas xanthospila</i> (Champion, 1893)	Yes	Yes, abdomens	Yes	Probably	Yes	(Figure 2(f)) [7]
Coleoptera: Curculionidae: Hyperinae						
<i>Phelypera distigma</i> (Boheman, 1842)	Yes	Yes, heads	Yes	Yes	Yes	[24, 40, 41]
Diptera: Ceratopogonidae:						
Forcipomyiinae						
<i>Forcipomyia fuliginosa</i> (Meigen, 1818)	Yes	Yes, abdomens	Yes	Probably	Yes	[1, 11, 42–44]
Hemiptera						
Not specified	Not reported	Not reported	Not reported	Not reported	Not enough information	[11, 12]
<i>Ceroplastes</i> sp. (Coccidea), <i>Potnia</i> sp. (Membracidae), <i>Nephesa rosea</i> (Spinola, 1839) (Flatidae), <i>Derbe</i> sp. (Derbidae)	Roughly to not circular	No, mixed extremities	No	Unclear	No	[11]
<i>Antiteuchus tripterus</i> (Fabricius, 1787) (Pentatomidae)	Yes	Unclear, abdomens	No	No	No	[45]
<i>Parastrachia japonensis</i> (Scott, 1880) (Parastrachiidae)	Yes	Unclear, abdomens	No	No	No	[46]

TABLE 1: Continued.

Organism	1 Circular formation	Criteria 2 Best defended extremity at the periphery	3 Default rest position	Aggregation is defensive (not for nest protection)	Is the behaviour cycloalexy?	Reference
Hymenoptera: Tenthredinoidea						
<i>Bergiana</i> sp. (Cimbicidae)	Yes	Not reported	Not reported	Not reported	Not enough information	[1]
<i>Perga dorsalis</i> Leach, 1817, <i>P. affinis</i> Kirby, 1882 (Pergidae)	Yes	Yes, heads	Yes	Yes	Yes	(Figure 3(a)) [7, 11, 12, 47, 48]
<i>Pseudoperga guerini</i> (Westwood, 1880) (Pergidae)	Yes	Yes, heads	Yes	Yes	Yes	[49]
<i>Themos olfersii</i> (Klug, 1834) (Argidae)	Yes	Yes, heads	Yes	Yes	Yes	[1, 50]
<i>Dielocerus diasi</i> Smith, 1975 (Argidae)	Not reported	Not reported	Not reported	Unclear	Not enough information	[1, 50]
Hymenoptera: other superfamilies						
<i>Trigona</i> sp. (Apidae: Meliponinae)	Yes	Yes, heads	No	No	No	[1, 7, 11, 51]
Adult Hymenoptera, bees (Apidae), wasps (Vespidae), <i>Conomyrma</i> spp. and numerous other ants (Formicidae)	Some circular, some not	Yes, usually heads	No	No	No	[11]
<i>Apoica</i> sp. (Vespidae: Polistinae)	Yes	Yes, heads	Yes	No	No	[52–54]
“Parasitic Hymenoptera larvae and pupae [on] their host”	Yes	Unclear, abdomens	No	No	No	[11]
Lepidoptera: Papilionidae: Papilioninae						
<i>Papilio laglaizei</i> Depuiset, 1877	Yes	Unclear, heads	Yes	Not reported	Tentatively	[24, 55]
Lepidoptera: Saturniidae						
<i>Hylesia</i> spp. (Hemileucinae)	Unclear	Not reported	Yes	Probably	Not enough information	[7]
<i>Lonomia</i> spp. (Hemileucinae)	Yes	Probably, heads	Yes	Probably	Probably	(Figure 3(b)) [11, 56, 57]
<i>Arsenura</i> spp. (Arsenurinae)	Not circular	No, mixed extremities	Yes	Probably not	No	[1, 11].
Lepidoptera: other families						
Noctuidae and Sphingidae	Not circular	No, mixed extremities	Not reported	Probably not	No	[11]
Neuroptera: Ascalaphidae						
<i>Ascaloptynx fusciger</i> (McLachlan, 1891)	Yes, around twig	No, mixed extremities	No	Yes	No	[1, 11, 12, 58]
Thysanoptera: Phlaeothripidae						
<i>Anactinothrips nigricornis</i> Hood, 1936 and <i>A. gustaviae</i> Mound & Palmer, 1983	Yes	Yes, abdomens	Yes	Probably	Yes	(Figure 5(b)) [59]
Non-insect arthropods						
<i>Phronima sedentaria</i> (Forskål, 1775) (Crustacea: Amphipoda: Hyperidea)	Yes	Unclear, heads?	Yes	No	No*	[24, 60, 61]
Platydesmidae, Unidentified sp. (Myriapoda)	Yes	Unclear, abdomens	Not reported	Not reported	Tentatively analogous	[24, 62]
Vertebrates						
Some ungulates, for example, Muskoxen <i>Ovibos moschatus</i> (Zimmermann, 1780)	Yes	Yes, heads	No	Yes	No	[1, 11, 12]
Antarctic penguins	Yes	Unclear, backs	Yes	No	No	[12, 63]

*These taxa are maternally defended and pose a special challenge to the definitions of cycloalexy (see Section 3.2.5).

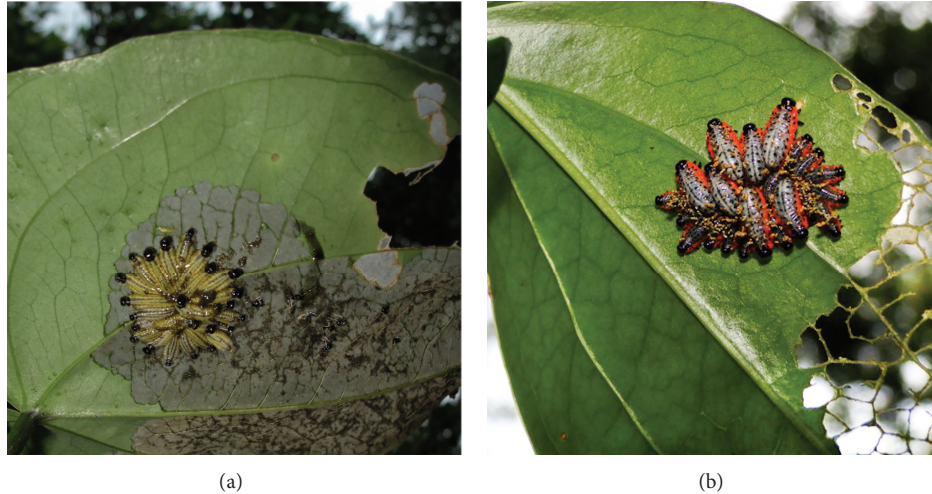


FIGURE 1: Cycloalexy with heads outwards in shining leaf beetle larvae (Criocerinae). (a) Larvae of *Lema* sp. at rest, photograph in Potrerillos del Guendà, Dept. Santa Cruz, Bolivia, © D. Windsor. (b) *Liliocerus nigropectoralis* larvae in Taiwan. Seven larvae are distinctly larger and appear to be from a different cohort than the other twelve. Photograph taken in Yangmingshan National Park on 2 August 2011, by 劉達偉 (Liu Dá Wēi), and licensed under the Creative Commons 3.0 Taiwan (CC BY-NC 3.0 TW).

3.2.2. Mixed Head Orientations. Larvae of the owlfly *Ascalop-tynx furciger* (McLachlan, 1891) (Neuroptera: Ascalaphidae) are gregarious. After eclosion and their first meal of abortive eggs, they settle head-downwards on and around the twig on which they were laid [58]. Jolivet et al. [1] deem the behaviour of *A. furciger* is “not strictly cycloalexy but related to it” since the owlfly larvae all point in the same downward direction: this does not meet the second criterion of the revised definition. We agree with Jolivet and Verma [12] that cycloalexy exists around twigs and is not restricted to flat surfaces. However, even on small branches, cycloalexic larvae collectively orient their heads either outwards or inwards, but not both. This is true for larvae of *Perga* sp. (Hymenoptera: Tenthredinoidea: Pergidae) (Figure 3(a)), *Omaspides tricolorata* (Boheman, 1854) [39], and this arrangement is retained in the pupae of *Omaspides pallidipennis* (Boheman, 1854) (Chrysomelidae: Cassidinae) [37]. For owlfly larvae, heads form the periphery at the bottom of the aggregation and abdomens are at the periphery on top, but unlike Cassidinae or *Coelomera* larvae, their abdomens are more vulnerable. It is more accurate to describe the behaviour as unidirectional defence rather than circular defence; larvae are only protected from predators walking up to the group. Secondly, larvae also feed while, in this position, making it a passive hunting formation and not only a resting position [58]. Because they do not meet the second and third criteria, we question reports of cycloalexy in Neuroptera [7, 11, 12, 64].

3.2.3. Nonresting Behaviours. As stated in the third criterion, cycloalexy is adopted preemptively by animals at rest. When immature insects are active and feeding, the circular formation is normally broken (Figure 4). Larvae of *Plagioderma versicolora* (Laicharting, 1781) and other *Plagioderma* species form a loose circle when feeding and at rest, with individual

larvae not consistently facing outwards or inwards [22, pers. obs.]. Hence their formation is not an example of cycloalexy. Their formation is not only adopted at rest but also while feeding and is often influenced by the shape of the leaf, with multiple “feeding rings” on larger leaves [22]. Some authors [11] feel that cycloalexy facilitates feeding in *P. versicolora* as well as in sawflies. Larval aggregations can increase feeding efficiency through synchronized, coordinated, and spatially concentrated feeding [23–25]. The size of *P. versicolora* groups does not influence survival of larvae, but does help with feeding [25]. Thus, available evidence suggests grouping in *P. versicolora* is related principally to the process of feeding rather than defence.

3.2.4. Nondefensive Behaviour. Cycloalexy is a defensive behaviour; it protects individuals from predation or parasitism. Yet, some reported behaviours are not defensive. Such is the case for huddling in Antarctic penguins, where the huddle is a resting behaviour, usually with heads inwards, but it is for heat conservation rather than defence [63]. For these reasons, we disagree with Jolivet and Verma [12] that penguins are cycloalexic.

To conclusively prove the defensive value of a behaviour, ecological studies are needed. Yet, for many species, the defensive value of cycloalexy has been inferred from anecdotal evidence or personal observations or has simply been presumed. For example, the defensive value of cycloalexy in *Phelypera distigma* larvae is supported by the following statement: “*P. distigma* larvae are not harvested by polistine wasps, ants, spiders, and other generalist predators that readily harvest caterpillars in dry forest habitats (D. H. Janzen, pers. obs.)” [65].

Rather than rejecting the many reports of cycloalexy on the basis of insufficient ecological studies, we propose that defensive nature of the aggregation can be accepted if the

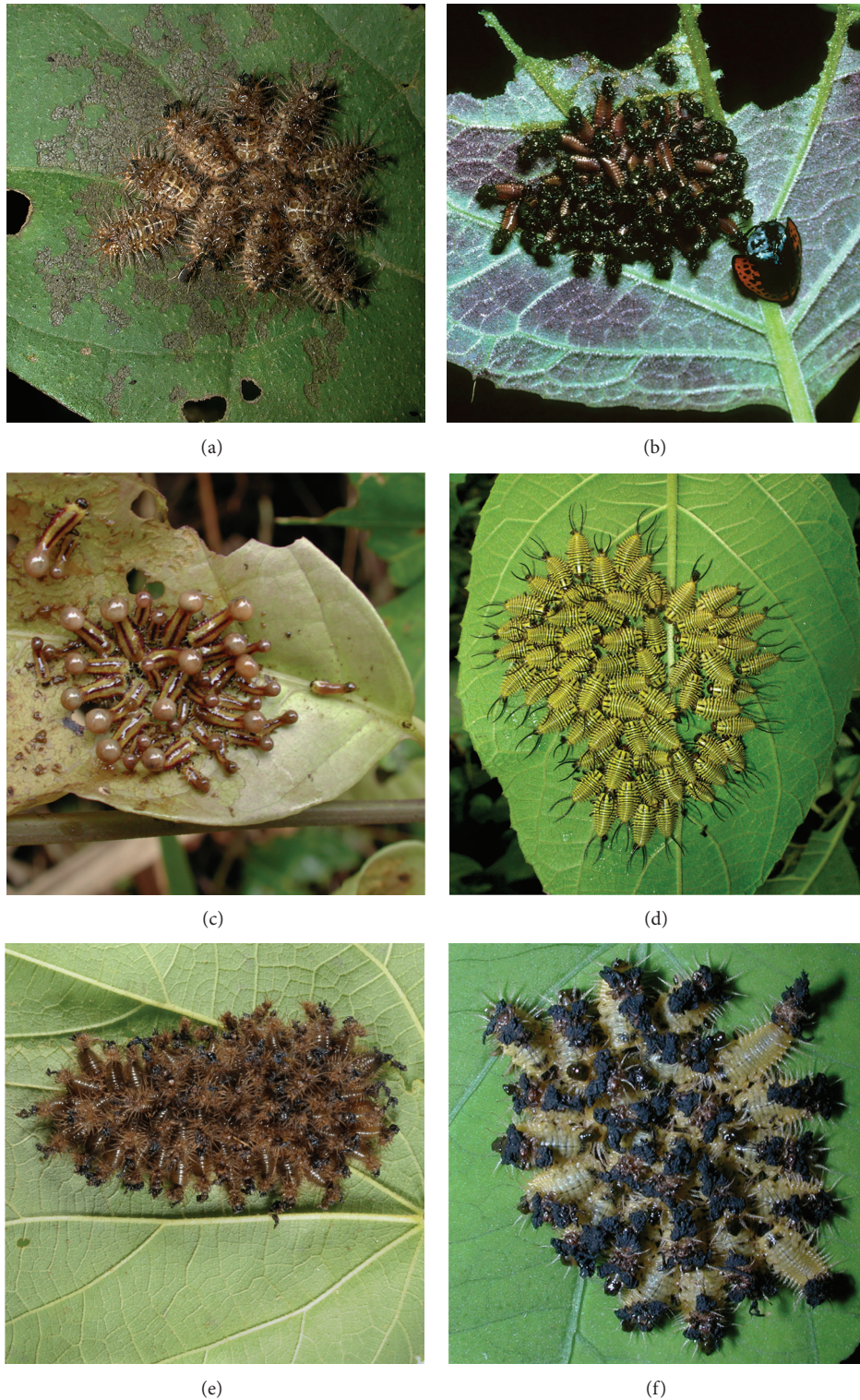


FIGURE 2: Cycloalexy in tortoise beetle larvae. (a) *Cistudinella foveolata* (Ischyrosomychini) larvae on host *Cordia alliodora* (Ruiz & Pav.) Oken. Gamboa, Colón Province, Panama; (b) *Eugenysa coscaroni* (Eugenysini) larvae and mother on host *Mikania guaco* Bonpl. (Asteraceae), Cerro Campana, Panama Province, Panama; (c) *Nuzonia* sp. on host *Maripa nicaraguensis* Hemsl., Chiriquí Grande, Bocas del Toro Province, Panama; (d) *Physonota alutacea* (Ischyrosomychini) larvae on host *Cordia spinescens* L., Gamboa, Colón Province, Panama; (e) *Polychalma multicava* (Goniocheniini) larvae on host *Helicteres guazumaefolia* Kunth. (Sterculiaceae), Gamboa, Colón Province, Panama; (f) *Stolas xanthospila* (Mesomphaliini) larvae on host *Turbina corymbosa* (L.) Raf. (Convolvulaceae), Cerro Campana, Panama Province, Panama; all photographs © D. Windsor.

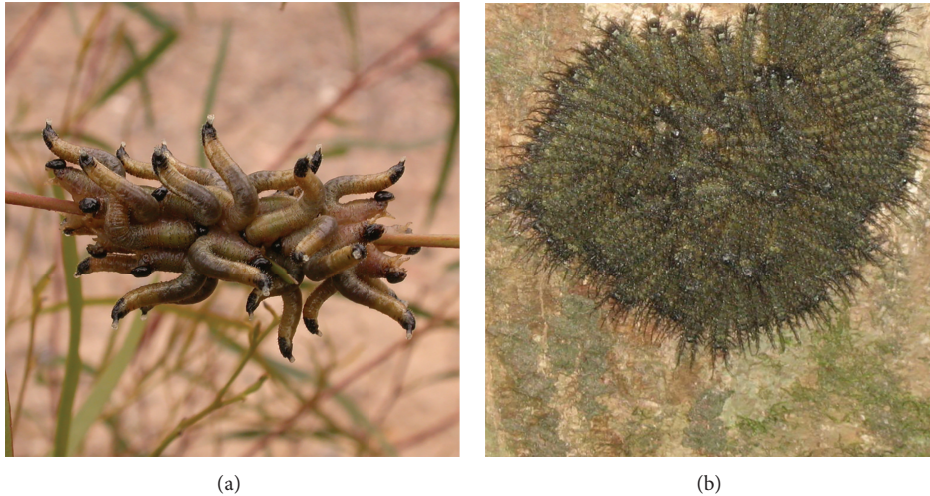


FIGURE 3: (a) Larvae of *Perga* sp. (Pergidae) rest aggregated in a cycloalexic formation. Even around a stem of their host plant, *Eucalyptus* sp., spitfire larvae rest with their heads outwards, Black Mountain, Canberra, ACT, Australia. Photograph by Donald Hobern on 24 May 2010 (CC BY 2.0). (b) Probable cycloalexy with heads pointing outwards in caterpillars of *Lonomia* sp. (Saturniidae: Hemileucinae) on tree trunk in Peru. Photograph taken near Pongo de Caynarachi, Lamas, San Martin, Peru, and reproduced with the author's permission © Marc Diaz Rengifo (Universidad Nacional Federico Villarreal, Lima, Perú).

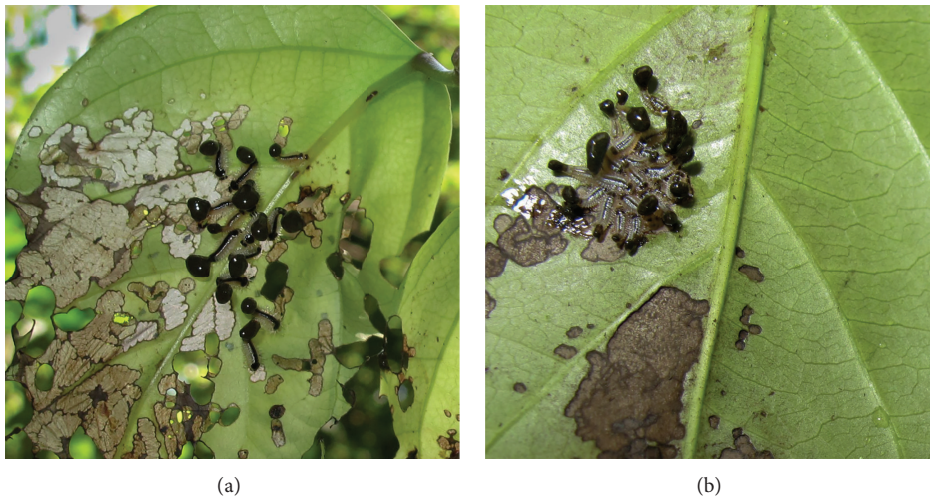


FIGURE 4: *Coptocyclus dolosa* larvae, Potrerillos del Guendà, Dept. Santa Cruz, Bolivia. (a) when active, feeding, or moving; (b) at rest. © D. Windsor.

animals meet the other criteria: they are in a circle, taken preemptively with defensive armature uniform at the periphery. When ecological studies are conducted, if defensiveness is disproved, then the behaviour is another type of aggregation and not cycloalexy. This is the case for larval aggregations of *Plagiodera versicolora*: ecological studies were conducted and the survival of larvae is not significantly influenced by group size [25].

3.2.5. Circular Formations That Do Not React to Threats. The original definition of cycloalexy requires coordinated movements in response to threats [1]. We disagree with this requirement: in some larvae with passive protection, like the exuvial or exuvio-fecal shields of tortoise beetles, the

circular groups do not always use coordinated movements when threatened by predators. For example, the larvae of *Conchyloctenia punctata* (Fabricius, 1787) (Cassidinae) are passively protected by their shields but do not have coordinated reactions to threats [30]. In our opinion, larvae of *C. punctata* meet the basic criteria of cycloalexy. Although coordinated group reactions to threats are an indication of the defensive nature of the group, we propose it is not an essential criterion for cycloalexy.

The removal of this criterion is also important for several taxa in which the larvae receive maternal care. Cassidinae larvae in maternal care species (e.g., species of genera *Acromis*, *Omaspides*, *Paraselenis*, and *Eugenysa*) generally have reduced fecal shields and do not always react defensively

when threatened. Larval grouping in these species can be considered as increasing the efficiency of maternal guarding. In these cases, all criteria of the revised definition are met: larvae are in a circle, the best defended extremity is always at the periphery, and the circle is the default resting position. Thus, we consider larval aggregations in these maternal care species as further examples of cycloaexy (Table 1).

Similarly, larvae of several chrysomelinae rest in tight circular groups with the heads pointing inwards: *Doryphora paykulli* (Stål, 1859), *D. reticulata* Fabricius, 1787, *Platyphora microspina* (Bechyně, 1954), *P. selva* Daccordi, 1993, *Proseicela vittata* (Fabricius, 1781), *P. spectabilis* (Baly, 1858), *P. bicrucata* Jacoby, 1880 and *Pr. sp. nov. "Yasuni"* [15]. All these species also have maternal care, and when disturbed, larvae do not have coordinated defensive reactions. Instead, the mother acts as the defensive element of the formation (Figure 5(a)) [15]. Is this behaviour still cycloaexy? In other words, should the defensive element obligatorily be found, at least in part, in the larvae? To this question, our answer is yes, through the second criterion. In Cassidinae larvae, the furca and shield are obvious defensive attributes positioned at the periphery. In Chrysomelinae, the best defended extremity is less obvious. Cycloaexic larvae of nonmaternal care Chrysomelinae face outwards. Their best defended extremity is the head and thorax, through regurgitation and biting [7]. We hypothesize that, in species with maternal care, the individuals face inwards not because the best defended extremity is the abdomen but because of herding by the mother, and thus, these species do not meet the second criterion of the revised definition. Ultimately, only ecological and evolutionary studies will provide a clear answer.

3.2.6. Adult Insects. We use *Apoica* as an example even though cycloaexy was not explicitly reported in this genus. During the day, these nocturnal wasps rest on the circular or nearly circular lower surface of their nests [52–54]. The wasps rest facing outwards, resulting in a circular formation that could loosely be termed cycloaexy. When disturbed, the formation breaks up as wasps fly off the nest. Even though this behaviour meets several criteria of the revised definition, we argue it is not cycloaexic because the shape of the nest or nest entrance explains the circular formation. In a similar fashion, stingless bees of genus *Trigona* (Apidae: Meliponinae) are not cycloaexic as suggested by Vasconcellos-Neto and Jolivet [7]. In this case, fully developed individuals are not even at rest: in most Meliponinae, the nest entrance is protected by bees positioned in or around the entrance tube and, at night, the entrance is closed [51]. The bees are not resting but are actively guarding and the ring formation is an artefact of the nest entrance shape.

These examples motivate limiting and specifying cycloaexy as a formation taken by individuals, whether immature or adult, for increased individual and mutual defences, thus excluding formations taken for defence of a nest, brood, or food stores. We argue that evolution of circular nests and resource guarding may have little to do with the evolution of cycloaexy.

3.2.7. Circular Defence in Vertebrates and the Selfish Herd. Several authors compare cycloaexy to the “circle-the-wagons” formation employed by American pioneers to defend themselves against Native Americans [1, 11, 12, 24]. In Jolivet et al. [1] and Jolivet and Verma [12], the authors discuss behaviours analogous to cycloaexy in vertebrates: muskoxen (*Ovibos moschatus*), eland (*Taurotragus oryx* (Pallas, 1766)), elk (*Cervus canadensis* (Erxleben, 1777)), and penguins. The authors do not provide citations for the behaviour in eland or elk and cite Wilson [4] for descriptions of this behaviour in muskoxen and penguins. Wilson [4] does not mention penguins in this manner but does mention similar behaviours in several terrestrial ungulates and killer whales (*Orcinus orca* (Linnaeus, 1758)) ([3, 66–69]; all page 45 in [4]). Wilson [4] describes elk grazing in a “windrow” formation but does not mention circular defence [70] and [4, page 45]. We agree that several vertebrates employ defensive circular formations analogous to cycloaexy. However, we would not broaden the definition to include these behaviours. Unlike invertebrates, mammals do not use circular defence when resting but take the formation when threatened. This does not meet the third criterion of the revised definition. In cycloaexic species, the circular formation is the main resting position. The circular defence of vertebrates is reactive, while cycloaexy in invertebrates is largely preemptive.

Hamilton used herding animals as an example of how individuals may form a group to lessen individual chances of falling to a predator without reducing overall predation [71]. Hamilton then cited the circular defence of muskoxen as a potential exception to the selfish herd theory but attributes it to selfish reasons: “they are probably connected on the one hand with the smallness of the risk taken and, on the other, with the closeness of the genetical relationship of the animals benefited” [71]. Because cycloaexy may lessen both overall and individual predation risk, it can also be considered selfish. Cycloaexy can be explained by animals exploiting the best defended extremity of nearby individuals. The preemptive aspect of arthropod cycloaexy also distinguishes it from muskoxen circular defence and Hamilton’s selfish herds and may therefore provide interesting systems for study of group defence.

3.2.8. Cycloaexy in Immature Hemimetabolous Insects. We report cycloaexy in *Anactinotrips nigricornis* Hood, 1936 (Thysanoptera). We observed a group of 14 thrips, in their pupal instar, forming a tight circle with abdomens outwards on a leaf of the woody vine *Maripa panamensis* Hemsl. (Convolvulaceae) (Figure 5(b)). When disturbed, the threatened individuals and those beside them waded their abdomen. When disturbance continued, a brown liquid was exuded and formed a droplet at the end of the abdomen. The group was then further disturbed and the individuals dispersed. Approximately an hour later, the thrips had reassembled in a circular resting formation. In the lab, after the final moult, the adult thrips dispersed in the container in which they were kept. Similar observations were made in another species of the same genus: the thrips *A. gustaviae*, Mound and Palmer,

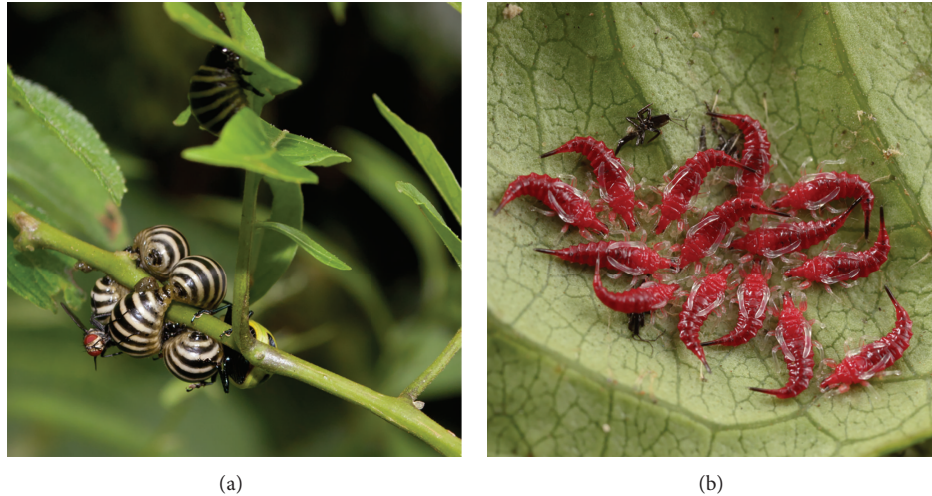


FIGURE 5: (a) Larvae of *Proseicela spectabilis* Baly (Chrysomelidae: Chrysomelinae) at rest encircling the stem of their host plant with tachinid fly at the bottom left of the cluster and the adult female beetle on the opposite side. Photograph taken in Reventador, Napo Province, Ecuador, © G. Dury. (b) Circular resting position in Panamanian thrips (*Anactinothrips* sp.) on *Maripa panamensis* Hemsl. (Convolvulaceae). Photograph taken 24 April 2013, on Cerro Campana, Panama. © G. Dury.

1983, rest in bivouacs and exude a defensive liquid from their abdomen when disturbed [59, 72].

The behaviour was observed in the mobile pupal stage rather than in the larvae. This goes against the original definition but meets all other criteria and assuming it is defensive, we consider the behaviour is cycloalexy. Thus, we propose to remove the taxonomical restriction of the original definition.

3.3. Common Traits of All Cycloalexic Species. When the revised definition of cycloalexy is strictly applied, a set of traits common to all species becomes apparent. Foremost, all cycloalexic species are insects with gregarious immature stages. Gregarious lifestyles have implications in terms of cooperative feeding and continued group cohesion through chemical, tactile, or acoustic communication [24].

To date, all cycloalexic species appear to use chemical defences of one sort or another. The cycloalexic larvae in genera *Lema* (Criocerinae) and *Platyphora* (Chrysomelinae) regurgitate when threatened [7, 9]. The larvae of *Forcipomyia* have paired setae on the head, thorax, and abdomen that exude hygroscopic substances that repel ants [44]. The chemical defences of gregarious *Lonomia* caterpillars are so potent that the resulting trauma caused by venom injected from their setae can be lethal to humans [73]. Most tortoise beetle larvae carry an exuvial or exuvio-fecal shield on the furca of their eighth abdominal segment which serves as a mechanical or chemical barrier against predators [74–76]. In all cases, the best protected extremity faces outwards.

Furthermore, all the species that exhibit cycloalexic behaviour are miniature grazers, and most feed on leaves. This is the case for cycloalexic caterpillars, and larvae of sawflies [47], weevils, and leaf beetles [7, 40]. Some feed

on fungal hyphae, such as *Forcipomyia fuliginosa* (Meigen, 1818) midge larvae [42], and the rest graze on lichen, like *Anactinothrips gustaviae* thrips [59].

Gregarious lifestyles, chemical defence, and grazing groups of immature insects are all traits of Costa's [24] "larval herd" syndrome of group living. Like cycloalexy, parental care is only present in some of these larval herds [24]. Possibly, the slow-moving and exposed lifestyle of these immature insects makes them more vulnerable to predators and parasitoids [24, 77]. Increased threats probably explain the multiple defences of insect herbivores, including chemical defence whose evolution generally precedes that of aggregation [78].

4. Conclusion

Several immature insects exhibit cycloalexy, a behaviour whose definition we have amended to: "A preemptive defence employed at rest, where individuals form a circle with their best defended extremity exposed at the periphery. Sometimes remaining individuals rest at the centre of the circle."

In leaf beetles (Chrysomelidae), cycloalexy with abdomens oriented outwards is found in one genus of skeletonizing leaf beetles (Galerucinae: *Coelomera* spp.), at least fifteen tortoise beetle genera (Cassidinae), two genera of shining leaf beetles (Criocerinae: *Lema* and probably *Liliocercis*), and several genera of broad-shouldered leaf beetles (Chrysomelinae: *Platyphora*, probably *Chrysophtharta* and tentatively *Eugonycha* and *Pterodunga*). Cycloalexy with heads outwards is found in some sawflies (Tenthredinoidea: Pergidae: *Perga* spp. and Argidae: *Themos olfersii* (Klug, 1834)) of Australia and Brazil. Social caterpillars often form aggregations, but

these aggregations are rarely cycloalexic. However, caterpillars of *Lonomia* spp. (Saturniidae: Hemileucinae) are probably cycloalexic and *Papilio laglaizei* Depuiset, 1877 (Papilionidae) are tentatively cycloalexic. One weevil *Phelypera distigma* (Boheman, 1842) (Curculionidae) is cycloalexic and one midge *Forcipomyia fuliginosa* (Ceratopogonidae) exhibits cycloalexy. We propose that some immature thrips are also probably cycloalexic and suggest formally changing the definition of cycloalexy to remove taxonomical restrictions so that any animals that meet all other criteria of the definition can be included. New instances of cycloalexy will undoubtedly be discovered. For example, Platydesmid millipedes sometimes aggregate in a tentatively analogous fashion.

Several reports of cycloalexy do not meet one or more of the revised definition criteria, including reports of cycloalexy in feeding aggregations of Hemiptera and larvae of Hymenopteran parasitoids. The behaviour has also been mistakenly attributed to adult Hymenoptera, for example, stingless bees (Apidae: Meliponinae), ants (Formicidae), and wasps (Vespidae), guarding their nest. This is active protection of a nest and not cycloalexy. Similarly, the term has been applied to the circular assembly of an amphipod crustacean which helps the mother herd the larvae. Owlfly larvae (Neuroptera: Ascalaphidae: *Ascaloptynx furciger*) form unidirectional defensive groups which are not cycloalexic, allowing larvae to feed without changing position. Defensive circles are sometimes observed in mammals: muskoxen, eland, water buffalo, red deer, and killer whales. Contrary to cycloalexy, the defensive formations in these mammals are a reaction to imminent threat. Other vertebrates, like penguins, huddle to reduce heat loss.

Application of a more precise definition of cycloalexy, as provided by Jolivet et al. [1] and revised here, may make unravelling the evolution of cycloalexic behaviour more tractable. Much remains to be learned about whether larval aggregation, cycloalexy, sequestration of plant metabolites, and maternal care are alternative defensive strategies or are honed evolutionary responses to particular threats. Chrysomeline leaf beetles are an ideal group for using phylogenetic reconstruction and character analysis of these behaviours to unravel the number of independent evolutionary origins of cycloalexy and larval aggregation.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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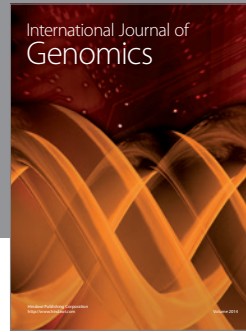
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