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REVIEW

Reviewing Social Facilitation In Insects Over The Past 30 Years

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Abstract

Social facilitation is a phenomenon in which individuals from a group show behavioral changes due to the presence of other organisms of the same species. This happens through group interaction between these individuals, later increasing in frequency or intensity. Social facilitation studies began with humans but later extended to other species, including insects. The concepts of social facilitation in insects developed over the last 30 years are reviewed here. To that end, bibliographic searches were carried out to determine when the term social facilitation first emerged, how it was described in the research, where and when it was applied, and how the concept is currently employed. There has been, however, a steady decrease in the number of published texts conceptualizing the term social facilitation during the last three decades. Nevertheless, the terms emergent behavior, collective behavior, and information exchange enabled expansion of the survey on social facilitation, indicating that study in the area remains broad. The orders Blattodea (cockroaches and termites) and Hymenoptera (ants, wasps, and bees) were the most represented among the surveyed publications, indicating the occurrence of social facilitation due to eusociality. Eusocial organisms demonstrate unique social interactions, which makes them likely objects of future social facilitation studies.

Introduction

Social organisms present changes in their behavioral patterns when they are in the presence of other organisms from the same species (Zajonc, 1965; Wilson, 1980; Decastro, 1995). When this behavior change is related to the increase in frequency or intensity of a particular behavior, this phenomenon is called social facilitation (Zajonc, 1965; Clayton, 1978; Keeling & Hurnik, 1996).

Among invertebrates, social facilitation is best explored among social insects (Wilson 1974; Fowler 1992; Reid et al., 1995), as several species increase or intensify their behaviors in response to a chemical or physical stimulus from conspecifics engaged in such behaviors (Wilson 1974; Fowler 1992; Reid et al., 1995). On the other hand, evidence of socially facilitated behavior in non-social insects is scarce and is mainly derived from data collected for other purposes (Prokopy & Duan, 1998).

In insects, social facilitation causes a variety of behavioral changes. According to Clayton (2008), Aristotle classified animals into solitary and gregarious, which presented social subcategories and included humans and social insects. Aggregation is the association of a species with perfect individualism, when each organism works for itself (e.g., grasshopper flocks, caterpillars; Gallo et al., 2002). Sociality or social organization among insects is divided by entomologists into different classifications. Eusocial insects are those which cooperate in the reproduction and division of reproductive labor and include Blattodea (cockroaches and termites) and Hymenoptera (wasps, ants, and bees). Subsocial insects, which have social habits that are not very strongly developed, have a lesser extension of cooperation and division of reproductive labor (Gullan & Cranston, 2008). Moreover, subsociality is the simplest form of social behavior and is present in many orders of insects, such as Dermaptera

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(earwigs), Thysanoptera (thrips), Hemiptera (true bugs), and Coleoptera (beetles) (Machado, 2007). In quasi-social behavior, a communal nest consists of members of the same generation, all of which contribute to brooding, with all females being able to lay eggs. In semisocial behavior, the communal nest also contains members of the same generation cooperating in the care of offspring. There is also a division of reproductive labor, with some females (queens) laying eggs, while their sisters or daughters act as workers and rarely lay eggs. Finally, solitary insects do not exhibit any social behaviors (Gullan & Cranston, 2017) and include Archaeognatha (bristletails), Odonata (dragonflies and damselflies), Ephemeroptera (mayflies), Plecoptera (stoneflies), Phasmatodea (stick and leaf insects), Mantodea (mantises), and Diptera (flies).

Social facilitation is a common phenomenon among termites and has been widely studied (Grassé & Chauvin, 1944; Springhetti, 1990). In this group, social facilitation can minimize the stress of individuals, and increase resistance to the effect of insecticides (Santos et al., 2004) and infections (Rosengaus et al., 1998). Furthermore, other studies have reported another behavioral change, whereby the size of the group can interfere in the frequency of interindividual behaviors, having consequences on longevity (Miramontes & DeSouza, 1996). Studies show that social facilitation increases termite survival time according to the group size in which these insects are confined (Miramontes & DeSouza, 1996; DeSouza et al., 2001; DeSouza & Miramontes, 2004; Santos et al., 2004).

The immune system of termites is also affected by social facilitation. In *zootermopsis angusticollis* (blattodea: termopsidae), there is a higher tolerance to fungus with increased group size (Rosengaus et al., 1998), while increased survival was observed in *cornitermes cumulans* even with insecticide application, demonstrating a greater resistance to such compounds (DeSouza et al., 2001). This effect is also perceived in the same species with different insecticides in field applications and controlled conditions in the laboratory (Santos et al., 2004).

In wasps there is a behavior of "stimulating" inactive individuals in the nest to collect resources. This stimulation can come either from the dominant female or other foraging females. This practice is not identified as recruitment, but as social facilitation because the individual's action generates or increases the activity of others without exhibiting an identical reflex to the efforts of the first (Wilson, 1975). Similarly, in *Atta colombica*, colonies with a high ant density worked harder than those with a lower density (Dussutor et al., 2007).

In some butterfly species, male aggregation often occurs to enhance resource acquisition and decrease the predation rate due to increased vigilance and dilution effect (Thorpe, 1964; Prokopy et al., 2000). In Diptera *Bactrocera tryoni*, females are frequently more attracted to males in larger aggregations than solitary males (Weldon, 2007; Burk, 1984; Mcdonald, 1987). In cockroaches, the group effect may also influence reproduction, as Gadot et al. (1989) found that when females are kept in groups, the oocytes mature faster than in solitary females. This is caused by the greater amount of juvenile hormone produced by the corpora allata of females confined in groups (Holbrook et al., 2000).

Thus, social facilitation has an ecological and economic importance that justifies a more detailed analysis of how it has been portrayed over the last 30 years.

Objectives

General Objective

To review social facilitation concepts over the past 30 years of insect research, their applications, and possible benefits for this group.

Specific objectives

I) Define when the term social facilitation arose;
II) Define where and when the term social facilitation is applied;
III) Define which concept is widely used nowadays.

Theoretical Reference

Brief History

Social facilitation in humans portrays a phenomenon first described by Triplett (1898), who performed a social psychology experiment to measure how long participants (children) took to pull a flag attached to silk cord around a four-meter course four times by turning fishing reels (Guerin, 1993). The results obtained in Triplett's experiments showed that participants in groups pulled the flag faster than participants who performed the task alone. Ultimately, Triplett's findings led to abundant research in this area.

The term social facilitation was coined by Allport (1924), but there was little research on the topic until the proposition of social facilitation impulse theory by Zajonc (1965). As it is a perceptible and not a palpable science, in his book "Social Psychology", Allport (1924) bases social facilitation on behavioral and experimental science, it being possible to perceive the phenomenon through observation.

The concept of social facilitation needs to be very well interpreted to understand the evolution of social behavior. In this perspective, the concepts of social facilitation were developed by authors such as Crawford (1939), Zajonc (1965), Milgram (1974), Clayton (1978), Markus (1978), and Klotz (1986), who, related the concepts according to the performance of social facilitation demonstrated in their research. The definition proposed by Crawford (1939) in his article "Social Psychology of the Vertebrates" considers social facilitation as any increase in individual activity resulting from the presence of another individual. In the concept proposed by Clayton (1978), the phenomenon refers to a behavior that is initiated or increased in frequency or intensity due to the presence of other individuals (Clayton, 1978).

Thus, social facilitation occurs when organisms of the same species alter their behavior due to the influence of other individuals in the environment (Milgram, 1974, cited by Weatherly et al., 1999). Besides being a form of cooperation, it is also considered the first sophisticated form of social communication (Klotz, 1986). Therefore, socially facilitated behaviors in animals that live in groups increase their efficiency in exploring for food resources and in protection against predators through the formation of aggregations and synchronization of reproduction (Clayton, 1978). Therefore, social facilitation represents a phenomenon in which group members improve their performance on a task and may increase task frequency.

Even in situations where individuals are not interacting with each other, some aspect of behavior can be modified (Weatherly et al., 1999). Thus, the theory of social facilitation refers to the influence on behavior among individuals in the presence of others (Zajonc, 1965; Markus, 1978; Guerin, 1993).

The Application of Social Facilitation in Animal Groups

Several animal behavior studies on this phenomenon have demonstrated the influence of the presence of conspecifics on the behavior of birds (Rajecki et al., 1976; Mason & Reidinger, 1981; Keeling & Hurnik, 1996); turtles (Meylan et al., 1990); lizards (Stamps, 1991); mammals (James, 1953; Levine et al., 1974; Dindo et al., 2009); gerbils (Forkman, 1991); arthropods (Hosey et al., 1985; Katvala & Kaitala, 2003; Chabaud et al., 2009); mollusks (Baur & Baur, 2000); social species such as wasps (Parrish & Fowler, 1983; Fowler, 1992; Reid et al., 1995), bees (Grasse & Chauvin, 1944; Chauvin et al., 1985), Ants (E. G. Chen, 1937; Chauvin, 1944; Grasse & Chauvin, 1944; Lamon & Topoff, 1985; Klotz, 1986; Salzemann & Plateaux, 1988; Hölldobler & Wilson, 1991), and termites (E.G. Grasse & Chauvin, 1944; Grassé, 1946; Lenz & Williams, 1980; Williams et al., 1980; Afzal, 1983; Okot-Kotber, 1983; Springhetti, 1990); and non-social species such as crabs (Kurta, 1982), centipedes (Hosey et al., 1985), and scorpions (El Bakary & Fuzeau-Braesch, 1987).

Most vertebrates are gregarious at some level (Reiczigel et al., 2008), having a tendency to form various social structures such as shoals, cultures, flocks, or groups of conspecific individuals. Thus, the evolution of life history, morphology, and behavior of different taxa are altered by community life (Krause & Ruxton, 2002), which can, in turn, be altered by the ecology of the species (Smith et al., 2008) and by differences in the degree of sociality (Patriquin et al., 2010). The formation of groups occurs when the benefits exceed the costs. However, predation pressure is one of the main aspects responsible for forming groups (Alexander, 1974). The formation of groups with some degree of sociality, even for short periods, promotes benefits such as less energy expenditure for activities such as surveillance or foraging (Artiss et al., 1999).

Aggregations are an example of social facilitation. Master et al. (1993) found that *Egretta thula* (Snowy egret) obtained higher capture success and lower energy expenditure when foraging in aggregations than solitarily. As such, there is the reinforcement of food acquisition with less energy expenditure, benefiting survival due to the increase of the group, in addition to increased protection. Lee (1994) also discusses other benefits of group life such as care for offspring (e.g., birds), thermoregulation (e.g., penguins and bats), and information exchange (e.g., primates).

Being part of an aggregation reduces the predation risk for each individual in the group (Hamilton, 1971; Clayton, 1978; Wilson, 1975; Beck et al., 1999; Prokopy & Roitberg, 2001). When the group is larger, the survival of individuals increases due to the increased frequency of vigilance behavior, and the change in vigilance rate therefore varies with group size. This hypothesis became known as the group size effect (Elgar, 1989). Having more eyes capable of observing the environment and finding a predator more quickly dilutes the chance of being predated (Elgar, 1989; Lima, 1995; Lima et al., 1999). Detecting the presence of predators can be done individually or collectively, depending on the quality of information on the predators (Treves, 2000).

Protection against predators can occur in four ways: the ability to detect predators, dilution effect, confusion effect, and cooperative defense (Hamilton, 1971; Alcock, 2001; Krebs & Davies, 1996). The first corresponds to the ability to detect predators due to multiple observers. An example of this type of research is Bertram's (1980) study on groups of ostriches; the author found that when in groups, each individual spends less time watching compared to the time spent by the lone individual. Therefore, total group vigilance (proportion of time with at least one bird watching) increased slightly with group size, meaning each bird in the group has more time to feed.

In the second form of protection, Krebs and Davies (1996) assert that in defense by dilution effect, individuals dissolve the impact of a successful attack because there is a high chance that another individual will be preyed upon. For example, an antelope in a herd of one hundred individuals has only a one in a hundred chance of being the victim in an attack, which makes it attractive for the prey to be part of a group as the chance of being preyed on decreases with the size of the group (Krebs & Davies, 1996).

The confusion and dilution effects can explain the size of the group in the predation rate. Being in a group provides benefits for animals that are under predation, as it reduces the possibility of individuals in the group being attacked and killed. (Hamilton, 1971). This dilution effect (Hamilton, 1971) imputes that while individuals in a group are equally spaced and at the same distance from the predator, they must all have equal probabilities of being hunted and killed during an attack (Vine, 1971).

The third form of protection is the confusion effect, in which individuals positioned at the center of a group may be safer than individuals from the extremities. According to Hamilton (1971), if the predator captures the victims from the edges, each group member should look for a central position, hiding behind others.

Predators experience a kind of confusion when they attack a dense group of prey (Neill & Cullen, 1974) and this explains why predators direct their attacks to the edges of the group. The confusion effect is caused by the synchronized movement of individuals within a group, and may increase their survival (Pitcher & Parish, 1993).

The fourth protection against predators emphasizes cooperative defense, whereby individuals from the same group jointly attack a predator, as in the case of mobbing in birds (Lee, 1994).

Observing the previously described defense strategies, the predator will get more success if it focuses its attack on small groups and solitary individuals. Thus, not only does living in a group prove beneficial, but the size of the group and the location of the animal within it also has an influence (Alcock, 2001).

Another positive aspect of group living is collaboration in exploring for food resources, both by increasing the probability of finding or capturing the resource and in the cooperative defense of food sources (Krebs & Davies, 1996). For example, when predators act in groups, they can catch larger or faster prey. When prey is aggregated, predators use collective hunting strategies to isolate a prey from its companions and chase it until subjugating it.

Social facilitation is also involved in the mechanism that generates synchrony as an individual's behavior can cause the same behavior in others and thus generate synchrony, increasing the benefits of group life and allowing it to be more cohesive. To support this suggestion, Coté et al. (1997) use the fact that synchrony is greater at the beginning of an outbreak of activities than at the end, with social facilitation contributing to starting the activity. In some species, movement synchrony also has a vital social component. Males that need to show off for females during sexual selection frequently exhibit synchronous behaviors in relation to the group, as in the case of synchronous light emission observed in fireflies, vocalization choirs in frogs, displays in bird leks, and vocal disputes in ungulates (Krebs & Davies, 1996). In the case of amphibians, it was observed that in addition to the synchronized vocalization of frogs functioning as an attraction, it also hindered their location by predators (Grafe, 2003).

Synchronous behavior has been detailed in the groups Arthropoda: Insecta (Buck, 1988), Chordata: Fishes (Breder, 1967; Partridge, 1982), Pterosauria (Greenberg, 2000), and Mammalia (Fellner, 2000; Ruckstuhl, 1999; Byrne, 2000). Many functions of this behavior can be proposed, all of which are correlated with the benefits of group life: increased vigilance, predator avoidance, and communication (Fellner, 2000). Social facilitation is often present in the early stages as it initiates most synchronous behaviors.

Social facilitation can also alter the behavioral repertoire of species; for example, when certain bird species are connected with a novel object next to their food resource, they usually show a neophobic reaction (Greenberg & Mettke-Hofmann, 2001). In such a situation, feeding occurs more easily in the presence of group companions in parakeets (*Melopsittacus undulates*) and zebra finches (*Taeniopygia guttata*) (Coleman & Mellgren, 1994; Soma & Hasegawa, 2004). Social facilitation of the exploration of new objects has also been described in crows (*Corvus corax*), which showed greater interest in a new object when tested in dyads compared to those tested individually (Stöwe et al., 2006). In tadpoles of the species *Bufo bufo*, exploration activity was increased in group individuals. (Griffiths & Foster, 1998).

In mollusks, there is a higher growth rate in paired and semi-paired individuals during the juvenile stage. This behavior can be interpreted as a strategy correlated with the hypothesis of guaranteed reproduction (D'ávila & Bessa, 2005; Carvalho et al., 2009). Thus, in the absence of conspecifics for mating, *Leptinaria unilamellata* (snail) demonstrates the capacity to delay sexual maturity by slowing its growth rate (Alhadas, 2014). However, in the presence of conspecifics, their growth is accelerated, leading them to reach sexual maturity earlier and ensuring cross-fertilization (Alhadas, 2014). Thus, social facilitation interferes with the life history of *L. unilamellata*, stimulating growth before sexual maturity (Alhadas, 2014).

Animals can influence the behavior between individuals of the same species in different ways and social interaction takes into account a process capable of promoting behavioral changes of great adaptive value (Galef, 1996). Group individuals learn new skills and increase the ability to obtain resources. This happens, for example, when males group together to attract more females or explore new objects by acquiring more food and obtaining information from their activities or the activities of other individuals through social learning (Clark & Mangel, 1984; Clark & Mangel, 1986; Giraldeau et al., 1994; Giraldeau, 1997).

Therefore, social facilitation benefits the most diverse groups of animals, extending to several areas such as feeding, reproduction, object recognition, and protection.

Social Facilitation in Insect Behavior

In eusocial insects (termites, bees, wasps, and ants), social facilitation affects the behaviors of organisms and their interactions. Lenz and Williams (1980) observed the survival of termite groups (*Nasutitermes nigriceps*) in environments with abundant resources but different container sizes. They reported that survival and wood consumption was reduced with increasing container size. This indicates that survival is related to container size and group size in relation to the amount of food supplied. Grassé (1986) discussed the correlation between group size and termite longevity and pointed out that termite survival was better in those kept in optimal conditions, suggesting that food was available. In this context, group size and survival correlate with the amount of food.

Social facilitation highlights a common phenomenon widely studied in termites (Grassé & Chauvin, 1944; Springhetti, 1990), whereby the increase in survival in termites may also be explained by the increase in interactions related to group size, such as trophallaxis and food ingestion (Miramontes & DeSouza, 1996; Miramontes & DeSouza, 2008).

High food intake, however, is not the only factor in increased survival. Tolerance to food scarcity was observed in *Nasutitermes cf. aquilinus* (Blattodea: Termitidae) when in groups. In this study, mechanisms that reduced food stress increased the survival of individuals that were in groups but had no effect on isolated individuals (Miramontes & DeSouza, 1996). In termites of the species *Cornitermes cumulans*, the increase in survival may be due to an effect on physiology. When in groups, these insects present low lipase enzyme activity, decreasing the energy expenditure of lipids and increasing survival even under conditions of food stress (Santos et al., 2007). Muradian et al. (1998) verified a similar situation, in which the production of CO^2 per capita is reduced with an increase in colony size, also decreasing energy expenditure. Thus, social facilitation in termites affects the mechanisms that allow them to overcome physiological stresses such as hunger (Miramontes & DeSouza, 1996), disease (Rosengaus et al., 1998), or insecticide intoxication (DeSouza et al., 2001).

Social facilitation has also been reported among individuals of different species of Lepidoptera (Heymann & Buchanan-Smith, 2000; Otis et al., 2006). Lepidoptera males aggregate in moist soil to acquire nutrients, a phenomenon called "mud puddle". Individuals of the species *Papilio Glaucus* are attracted only by intraspecific baits, while representatives of the species *Battus philenor* exhibited intraspecific and interspecific attraction. Both species preferably landed in puddles demonstrating a very strong local valuation, which can be defined as a form of social facilitation (Otis et al., 2006).

In a study on the rosehip fly, *R. basiola* Oston Sacken, Robertson et al. (1995) reported that females landing on fruits that had received eggs and host labelling pheromone, were more likely to lay eggs in the presence of a conspecific ovipositor than in the absence of one and interpreted this discovery within an ecological evolutionary context. Apple larvae flies, *Rhagoletis pomonella* (Walsh), Drosophila flies, *Cydia pomonella* (L.) moths, and *Helicoverpa zea* moths (Boddie) were found to lay more eggs per female when kept in groups than when kept alone (Prokopy & Bush, 1973; Hilker 1989; Chess et al., 1990; Abernathy et al., 1994). Similarly, *Taeniopoda eques* Burmeister females of locusts have been shown to feed more frequently on a given plant when grouped with female conspecifics than alone (Howard, 1993).

Social facilitation in insects increases foraging efficiency, predator defense, and improves reproduction, colonization, competitive skills, and survival (Wilson, 1980). Thus, social facilitation is of fundamental importance for the insect group.

Materials and Methods

In the present study an active search was carried out using keywords in Portuguese on the Google Academic platform and in English on the CAPES Periodicals platform. The keywords used as the main basis were social facilitation and group effect. The terms group behavior, benefits, social life, group living, social communication, aggregation, and the name of each group were also taken into account to find articles in the various orders.

All terms used in Portuguese were also used in English, being social facilitation and group effect. The terms group behavior, benefits, social life, group life, social communication, aggregation, and the name of the insect order were also used. CAPES journals automatically included the term group facilitation when the term social facilitation was added. The use of keywords in Portuguese and English was of great importance in the search for articles because it enabled expansion of the process of collecting the data necessary for the research (Table 1).

The articles were sorted over three decades, from 1990 to 1999, 2000 to 2009, and 2010 to 2020. The articles were selected based first on the title, then the abstract, and finally, the full text. In this context, a considerable number of documents were found in both languages on the subject, enabling a detailed analysis to find the authors' concepts regarding social facilitation in each insect group during the three decades under analysis.

Searches were conducted with the order Blattodea and the infraorder Isoptera so that no loss of information occurred. This differentiation was necessary due to the change in taxonomy that included termites, which were previously part of the order Isoptera and are now part of the order Blattodea within the infraorder Isoptera.

Results and Discussion

The orders Notoptera, Mantophasmantodea, Ephemeroptera, Odonata, Dermaptera, Thysanoptera, suborder Homoptera, Neuroptera, Trichoptera, Siphonaptera, Mecoptera, Mantodea, Psocoptera, Phthiraptera, Phasmantodea, Embioptera, Zoraptera, Plecoptera, Zygentoma, Archaeognatha, Strepsiptera, Megaloptera, Raphidioptera, and Grilloblattodea had no published papers on social facilitation in the three decades. These orders do not present social behavior that favors the occurrence of social facilitation, which is possibly why they did not appear in papers on the subject (Table 1).

In Table 2, it can be observed that there was a reduction in publications on social facilitation over the 30 years, except for the order Orthoptera. This reduction is observed only for

Table 1. The data presented in the table indicate the searches carried out by keyword, on the Google Scholar and Periodical CAPES platforms, by order of insects, in the decades of 1990-1999, 2000-2009, and 2010-2020.

Group of Insects by Order	Total	1990 - 1999	Articles with subject matter on social facilitation	2000 - 2009	Articles with subject matter on social facilitation	2010 - 2020	Articles with subject matter on social facilitation
Ephemeroptera	129	4	0	26	0	99	0
Odonata	251	12	0	55	0	184	0
Orthoptera	334	10	0	91	0	233	1
Blattodea + infraorder Isoptera	500	18	3	132	11	350	14
Dermaptera	116	3	0	29	0	84	0
Thysanoptera	164	7	0	45	0	112	0
Hemiptera	823	12	0	189	2	622	6
Homoptera	282	12	0	105	0	165	0
Neuroptera	145	6	0	33	0	106	0
Coleoptera	1369	44	0	406	0	919	1
Lepidoptera	1128	18	0	362	10	748	8
Diptera	1512	37	3	370	10	1105	4
Hymenoptera	1485	49	9	383	21	1053	33
Tricoptera	124	1	0	30	0	93	0
Siphonaptera	62	5	0	16	0	41	0
Mecoptera	16	0	0	7	0	9	0
Mantodea	50	2	0	11	0	37	0
Psocoptera	55	5	0	14	0	36	0
Phthiraptera	43	0	0	6	0	37	0
Phasmatodea	25	1	0	4	0	20	0
Embioptera	27	2	0	4	0	21	0
Zoraptera	275	5	0	74	0	196	0
Plecoptera	93	4	0	16	0	73	0
Zygentoma	7	2	0	0	0	5	0
Archaeognatha	9	0	0	0	0	9	0
Strepsiptera	17	0	0	4	0	13	0
Megaloptera	45	3	0	5	0	37	0
Raphidioptera	21	0	0	7	0	14	0
Notoptera	0	0	0	0	0	0	0
Grylloblattodea	26	1	0	5	0	20	0
Mantophasmantodea	0	0	0	0	0	0	0

the term social facilitation, but other terms such as emergent behavior, collective behavior, and information exchange are being used. Publications in the area of social facilitation were observed in the following orders: Orthoptera, Blattodea + infra order Isoptera, Hemiptera, Coleoptera, Lepidoptera, Diptera, and Hymenoptera.

Regarding the total number of articles published by order, the percentage of studies on social facilitation was very small for the orders Coleoptera (0.073%) and Orthoptera (0.299%) but increased slightly for the orders Hemiptera (0.972%), Diptera (1.124%), and Lepidoptera (1.595%). The orders with the most published papers on social facilitation are Blattodea + infra order Isoptera (5.6%) and Hymenoptera (4.242%). Eusociality is present in these two orders, and it can be defined as social insects that are comprised of ants, termites and the more derivative groups among bees and wasps.

The organization of the society of eusocial organisms is composed of one or a few reproductive females, workers, and a large number of young (WILSON, 1974, 1975). Eusociality portrays the highest degree of social organization in animals that live in highly complex societies. Moreover, for Wilson (1974), eusocial organisms have the following characteristics:

care for offspring, overlap of more than two generations, and division of labor with differentiation between castes. The relationships of eusocial organisms are very intense and social facilitation is often observed. Because this is a high-frequency phenomenon in eusocial insects, they are a fantastic model for the study of social facilitation.

Eusocial insects present emergent behavior, which is associated with the plasticity of the division of labor in colonies, in addition to the most successful survival strategies in nature (Ferreira Jr & Bazzan, 2007). It can be said that through the aggregation of workers, the behavior of the colony emerges without any explicit planning or coordination (Ferreira Jr & Bazzan, 2007).

Table 2. Percentage of articles on orders found with the subject social facilitation in the analyzed decades.

Groups by Orders	Percentage found between the years 1990-1999	Percentage found between the years 2000-2009	Percentage found between the years 2010-2020	Total percentage of the three decades studied
Orthoptera	0%	0%	0.429%	0.299%
Blattodea + infra order Isoptera	16.66%	9.09%	4%	5,6%
Hemiptera	0%	1.06%	0.964%	0.972%
Coleoptera	0%	0%	0.108%	0.073%
Lepidoptera	0%	2.762%	1.069%	1.595%
Diptera	8.108%	2.702%	0.361%	1.124%
Hymenoptera	18.37%	5.483%	3.133%	4.242

Foraging of eusocial insects is related to the sharing of information, ranging from trail formation (Robinson et al., 2008) to collective decision-making (Nicolis & Deneubourg, 1999; Sumpter & Pratt, 2009). This information enables the establishment of collective foraging patterns, as the transfer of information occurs in the formation of trails in Hymenoptera (Deneubourg & Gossup, 1989; Dussutour et al., 2005).

Over the three decades, there has been a noticeable decrease in publications on social facilitation (Figure 1). Orders such as Lepidoptera, Diptera, and Hemiptera may group at some point in their lives, enabling social facilitation to occur at some vital stage. No publications were found for other groups with little or no sociality. The orders Coleoptera and Orthoptera had few publications over the 30 years, probably because they are not eusocial.

In the 1990s there was a greater number of publications on social facilitation. In this period the order Hymenoptera obtained the most published articles, followed by the order Blattodea plus the infraorder Isoptera, and the order Diptera. The other orders did not present publications in the period. This is due to the fact that there was a possible division of the term.

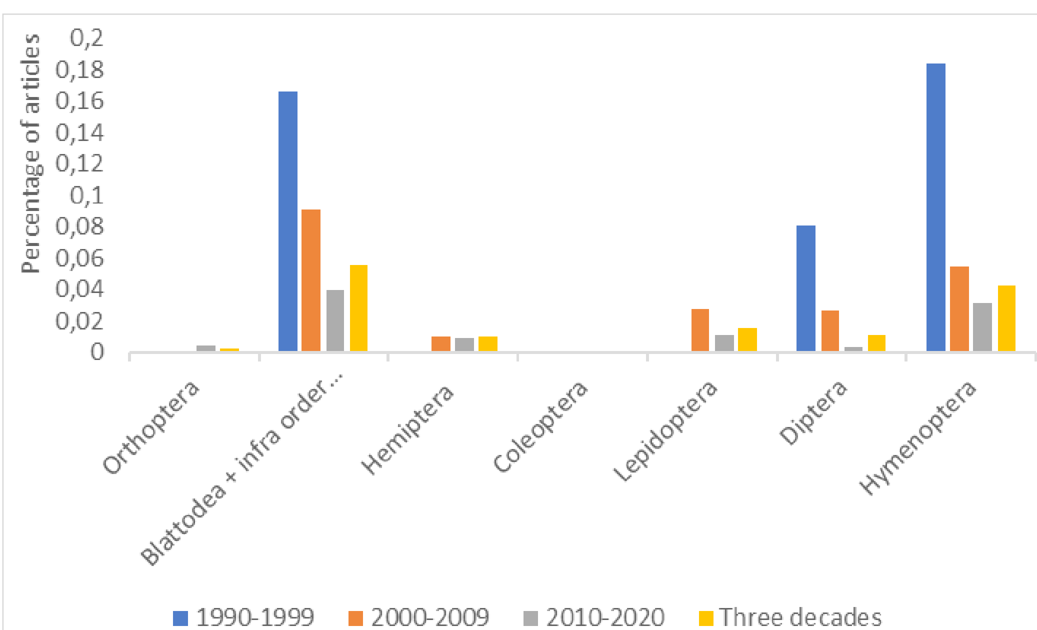

Fig 1. Graph representing the decades analyzed and the percentage of articles on the Orders that presented a subject on social facilitation.

Articles found separated by decade
Between the years 1990 – 1999

In 1996 an article on Isoptera was found: "The nonlinear dynamics of survival and social facilitation in termites". In this article the concept attributed to Wilson in 1980 was used as follows: Social facilitation is defined as the common patterns of behavior that are incipient or increased in rhythm or frequency by the presence or actions of other animals (Wilson, 1980). The following statement was also observed: Most classical studies of social facilitation focused on the performance of tasks by individuals, in contrast to individuals in groups (Chen, 1937).

Two articles on Diptera were found, one in 1998 with the title: "Ovipositional enhancement through socially facilitated behavior in *Rhagoletis pomonella* flies", which applied the concept, according to Clayton (1978), of the behavior of an individual which shows "an increase in the frequency or intensity of responses or the initiation of particular responses already in an animal's repertoire, when shown in the presence of others engaged in the same behavior at the same time". The second article with this theme from the year 1999 was entitled: "Facilitation in ovipositional behavior of *Bactrocera tryoni* flies", and the concept used was Clayton (1978).

In the order Hymenoptera, two articles were found. The first in 1992 with the title: "Social facilitation during foraging in *Agelaia* (Hymenoptera: Vespidae)", which used the concept of Wilson (1975), with the description: Social facilitation is the behavior initiated or increased by the action of another individual. The second was in 1998, entitled "Socially facilitated egglaying behavior in Mediterranean fruit flies", where Guerin (1993) considers social facilitation to be occurring when an individual increases or decreases its behavioral onset in the presence of another individual who does not necessarily interact with him. He also presented another concept from Clayton (1978), whereby the concept of facilitated behavior emphasizes that an individual engaged in such behavior initiates or increases the tension of behavior when in the presence of another individual who performs the same behavior.

The articles published in Portuguese in this period did not conceptualize social facilitation at any time. However, the term was mentioned or suggested throughout the texts with the terms group effect, group life, aggregations, and benefits.

Between the years 2000 – 2009

With the order Hemiptera, an article from the year 2003 was found with the title: "Conspecifics enhance egg production in an egg carrying bug", with the following concept: Social facilitation is the response of an individual to the presence of members of the same species (Vernon, 1995).

In the order Lepidoptera, an article published in the year 2006 was found with the title: "Local enhancement in mud-puddling Swallowtail butterflies (*Battus philenor* and *Papilio Glaucus*)" with the concept: Social facilitation is a phenomenon by which the behavior of an organism is initiated or increased in frequency or intensity due to the presence of other individuals performing the same behavior (Clayton, 1978).

An article about Isoptera was found in 2001 entitled: "Social facilitation affecting tolerance to poisoning in termites (Insecta, Isoptera)" with the concept: Social facilitation is defined as the common patterns of behavior that are initiated or increased in rhythm or frequency by the presence or actions of other animals (Zajonc, 1965; Wilson, 1980; Decastro, 1995). In the order of Hymenoptera in 2000 an article was found published with the title: "Social Wasp (Hymenoptera: vespidae) foraging behavior", using the definition by Wilson (1975) of social facilitation as the behavior initiated or increased by the action of another individual.

As in the previous decade, the articles published in this period did not change the concept of social facilitation, but the term and concept were mentioned or suggested throughout the texts.

Between the years 2010 – 2020

An article on Orthoptera was found in 2010 with the title: "The social context of cannibalism in migratory bands of the Mormon Cricket", with the concept: Social facilitation is an increase in the frequency of behavior in response to other individuals involved in the same behavior, with citations by Danchin et al 2008.

Only one article was found conceptualizing social facilitation for the Blattodea group in the year 2013 with the title: "Sensory cues involved in social facilitation of reproduction in Blattella germanica females", in which group living can alter the behavior, morphology, or physiology of individuals, generally promoting survival and greater fitness (Krause, Ruxton, 2002; Wilson, 1974). Furthermore, the phenomenon known as social facilitation, or grouping effect (Grassé, 1946; Gervet, 1968), is well described in many insect species as a form of group-induced phenotypic plasticity.

In addition, in the Lepidoptera group, two concepts of feeding facilitation were found in an article from the year 2019 with the title: "Caterpillars cooperate to overcome plant glandular trichome defenses". The first concept was that social facilitation of feeding can be defined in several ways, but the simplest and broadest definition, which makes no assumptions about an animal's motivational state, states that facilitation occurs when an individual's acquisition of food is facilitated by the feeding action of neighbors (Costa & Pierce, 1997; Weed, 2010; Ward & Webster, 2016). The second concept was that social facilitation of food can be considered a form of cooperation, defined as an interaction in which individuals confer mutual fitness benefits on each other (Barker et al., 2017).

An article was found in the Isoptera group in 2012 with the title: "Perspectives on the cohabitation of termites in termite nests (Insecta: Isoptera)”, in which social facilitation can be defined as the behavioral pattern of a given animal that is initiated or increased in rhythm and frequency by the presence or action of other animals (Zajonc, 1965; DeSouza et al., 2001).

In the Hymenoptera group, an article from 2015 was also found, with the title: “Individual differences in forage behavior of *Polistes versicolor* (Olivier, 1791) (Vespidae, Polistinae)”, in which social facilitation (Wilson, 1975) occurs because an action of a certain individual can generate or increase the activity of others.

The study “Descrição da atividade de forrageamento em Atta sexdens rubropilosa: compartilhamento de informação e seleção de tarefas” (Description of the foraging activity in Atta sexdens rubropilosa: Information sharing and task selection), from 2014, mentions collective foraging, whereby social facilitation behavior can be found during the process of searching for food. Collective foraging is an elaborate process and depends on a set of behaviors until its effective establishment (Carmo, D.V.; 2014). Recruitment behavior can still be found where social facilitation is present during the process. Planqué et. al. 2010, describe recruitment behavior as all communication that takes workers from the nest to a location where work is needed and may therefore involve more than just pheromone trail marking. In addition to the exchange of information that enables the activity of searching for food, foraging activity is mediated by the exchange of information, and to understand such an activity, the information mechanisms must be understood (Carmo, D.V.; 2014). The process of exchanging information leads to engaging in what will be the preferred task (Biesmeijer et al., 1998; O´Donnell, 2001, Fernandez et al., 2003; Pratt et al., 2002, Pratt, 2005, 2008; O´Donnell & Bulova, 2007), among several possibilities.

Another study on Hymenoptera, “On the trail with the Girl Scouts: how workers know the way forward”, from 2015, discusses collective behavior. Here, evidence of the emergence of complex collective behaviors from simple individual behaviors can be observed during foraging and recruitment in ant colonies (Silva, 2015). Recruitment behavior is a process in which a worker (recruiter) brings a certain amount of nestmates (recruited) to the food resource (Detrain et al., 1999;). The type of recruitment and the transmission of information about the quality and location of the resource is directly related to colony size. The exchange of information guarantees the maintenance of foraging between individuals (Silva, 2015). In the article excerpt, social facilitation is evident when individuals encourage others to look for food. When individuals encounter *Atta cephalotes* nestmates that are not laden with resources, they motivate the workers to collect resources (JAffé & Howse, 1979). For *Pogonomyrmex barbatus*, however, only successful foragers, that is, returning with resources, influence foraging activity (Gordon et al., 2002).

General Observations

The term social facilitation was coined by Allport in 1924 and the more comprehensive concept authored by Zajonc in 1965. Even though other authors are committed to conceptualizing social facilitation, they only add to the existing concept (Zajonc, 1965). The term social facilitation has been widely used in several studies, but it needed to be explained or conceptualized.

Another observation highlights that the concept should be applied in all articles that mention the term social facilitation to reliably convey information about the topic. In the analyzed studies, the concept of Clayton 1978 and Wilson 1975 were the most used. Sometimes another concept is attributed to reinforce a concept already used .

For the most part, the articles published in the last three decades have yet to conceptualize the term social facilitation, making reading and understanding the subject more difficult. During the 3 decades there has been a decrease in the number of published papers conceptualizing the term social facilitation. This reduction might be related to terms that use the same concept, such as emergent behavior, information exchange, and collective behavior. Papers such as “A review on the development of individual-based model in ecology” from 2016; “The role of personality variation, plasticity and social facilitation in cockroach aggregation” and “Experience of the signaller explains the use of social versus personal information in the context of sentinel behavior in meerkats” from 2018; “Peaceful behavior: a strategy employed by an obligate nest invader to avoid conflict with its host species” and “Statistical physics of liquid brains” from 2019; and “Emergent behavioral organization in heterogeneous groups of a social insect” from 2020 present articles on social facilitation in their bibliographies, indicating that social facilitation continues to be studied using new terms.

In “The role of personality variation, plasticity and social facilitation in cockroach aggregation”, from 2018, concepts of social facilitation were found, whereby social facilitation occurs when the presence of group mates affects the behavior of an individual and enables or causes individuals to engage in certain behaviors at a different rate, or to perform behaviors that they would not do if they were alone (Zajonc, 1965). Furthermore, social facilitation can affect how individuals within groups express personality traits in many ways, adding a layer of complexity (Webster & Ward, 2011). In “Emerging behavioral organization in heterogeneous groups of a social insect”, there is a conceptualization of social facilitation, but there is no author mentioning the term. In “The role of personality variation, plasticity and social facilitation in cockroach aggregation”, “Experience of the signaller explains the use of social versus personal information in the context of sentinel behavior in meerkats”, “Peaceful behavior: a strategy employed by an obligate nest invader to avoid conflict with its host species”, and “Statistical physics of liquid brains”, the terms emergent behavior, collective behavior, and information exchange were found and are directly related to social facilitation, which indicates that social facilitation continues to be studied but with different terms.

Final Considarations

The results show that this study made it possible to review the concepts of social facilitation over the last 30 years of research, its applications to insects, and possible benefits. The research also revealed a decrease in the publication of articles, despite being related to environmental ecological issues and the need to analyze the role of the importance of social facilitation in insect groups.

In the first decade studied, Clayton (1978) was the most mentioned among Wilson (1980); Chen (1937); Clayton (1978) (four times); Wilson (1975); and Guerin (1993). In the second decade, Clayton (1978); Vernon (1995); Zajonc (1965); Wilson (1975 and 1980); and DeCastro (1995) were each mentioned once.

In the third decade the authors who conceptualized the term were Danchin, Giraldeau and Cezilly (2008); Grassé (1946); Gervet (1968); Costa and Pierce (1997); Weed (2010); Ward and Webster (2016); Barker et al. (2017); Zajonc (1965); as well as DeSouza et al. (2001), who also appeared once each.

Clayton (1978) was mentioned five times in the first two decades, while Wilson (1975) was mentioned three times, once in each decade. Wilson (1980) was mentioned twice in the first two decades. Finally, in the last decade, Ward and Webster (2016) and Barker et al. (2017) mentioned the concept of social facilitation of food.

The orders Blattodea (infraorder Isoptera) and Hymenoptera were the most represented, indicating the occurrence of social facilitation due to eusociality. Eusocial organisms have unique social interactions, a characteristic that makes them objects of study for social facilitation.

The terms emergent behavior, collective behavior, and information exchange enabled expansion of the survey on social facilitation, indicating that study in the area remains broad.

Authors' Contributions

AA-F: Conceptualization, Investigation, Writing-Original Draft, Writing-Review & Editing.
CAS: Supervision, Project administration, Writing-Original Draft, Writing-Review & Editing.

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