

Significance and Control of the Poultry Red Mite, *Dermanyssus gallinae*

O.A.E. Sparagano,^{1,*} D.R. George,¹
D.W.J. Harrington,² and A. Giangaspero³

¹Faculty of Health and Life Sciences, Northumbria University, Newcastle upon Tyne NE1 8ST, United Kingdom; email: olivier.sparagano@northumbria.ac.uk

²Poultry Division, Chr. Hansen A/S, 2970 Hørsholm, Denmark

³Dipartimento di Scienze Agrarie, degli Alimenti e dell'Ambiente, Università di Foggia, 71121, Italy

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*Corresponding author

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Abstract

The poultry red mite, *Dermanyssus gallinae*, poses a significant threat to poultry production and hen health in many parts of the world. With *D. gallinae* increasingly suspected of being a disease vector, and reports indicating that attacks on alternative hosts, including humans, are becoming more common, the economic importance of this pest has increased greatly. As poultry production moves away from conventional cage systems in many parts of the world, *D. gallinae* is likely to become more abundant and difficult to control. Control remains dominated by the use of synthetic acaricides, although resistance and treatment failure are widely reported. Alternative control measures are emerging from research devoted to *D. gallinae* and its management. These alternative control measures are beginning to penetrate the market, although many remain at the precommercial stage. This review compiles the expanding body of research on *D. gallinae* and assesses options for its current and future control. We conclude that significant advances in *D. gallinae* control are most likely to come through an integrated approach adopting recent research into existing and novel control strategies; this is being combined with improved monitoring and modeling to better inform treatment interventions.

INTRODUCTION

The poultry red mite, *Dermanyssus gallinae*, poses a significant threat to egg-laying hens in many parts of the world, including the United States, Europe, Japan, and China (21, 90, 108, 123). Although in the United States the northern fowl mite, *Ornithonyssus sylviarum*, may be more abundant (121), elsewhere *D. gallinae* tends to predominate. Economic costs associated with both control and production losses due to *D. gallinae* have been estimated at €130 million per year for the EU egg industry, with similarly large sums in other regions (108, 119).

Research concerning all aspects of *D. gallinae* has increased in recent years; however, the last major review on this pest was published in 1998 (21). The growing body of work on *D. gallinae*, increasing economic importance of this pest, and recent changes to poultry production practices that may promote infestations in many countries make this the ideal time to review the biology of *D. gallinae* and particularly its current and future control. Although the bulk of literature presented originates from Europe, where much of the recent research effort on *D. gallinae* has been focused, the data and ideas presented have broader significance to all countries in which *D. gallinae* presents a threat. Sections focusing on *D. gallinae* control will be of relevance to those with an interest in poultry pest management per se, particularly of similar species such as *O. sylviarum*.

Morphology, Biology, Life Cycle, and Ecology

D. gallinae (Mesostigmata: Dermanyssidae) is a relatively small ectoparasitic mite approximately 1.5 mm in length and varies in color from gray to brown/red depending on feeding status. *D. gallinae* may display relatively high genetic variability (107). In some cases this is thought to be a consequence of pesticide-driven selection forcing adaptation to different treatment regimens between countries (76); *D. gallinae* possesses a number of genetic architectures that enable it to adapt rapidly to selective pressures (107). As a possible result of these traits, *D. gallinae* displays relative plasticity in terms of host specificity (see below), although it remains associated primarily with birds in general and laying hens in particular (21, 105).

Only minimal work has been conducted on genetic markers for *D. gallinae*, for which ITS2 PCR (internal transcribed spacer 2 polymerase chain reaction) experiments have given the best results to date (101). In the absence of molecular-based species determination, morphological characteristics can be used to distinguish *D. gallinae* from similar species such as *O. sylviarum* (27). In contrast to *O. sylviarum*, the majority of the *D. gallinae* life cycle is spent off the host where mites seek refuge in secluded areas, such as cracks formed by timber joints, aggregating together in response to both thigmokinesis and pheromone cues (29, 64). *D. gallinae* locates its hosts using a combination of temperature stimuli, chemical signals, and responses to vibration and carbon dioxide (55, 56, 128). Once on a host, mites feed for short periods of up to an hour, doing so every 2–4 days and typically (although not exclusively) during periods of darkness (79, 93). Larvae do not feed, and though adult males may, they are thought to do so only intermittently (21).

Complete development of *D. gallinae*, from egg to adult through one larval stage and two nymphal stages, typically occurs over two weeks, although it may take place in less than half this time (9, 78) (**Figure 1**). Conditions within poultry houses are well suited to *D. gallinae* population growth, where temperatures between 10°C and 35°C and high relative humidity (>70%) facilitate *D. gallinae* reproduction and development (78, 96). Consequently, weekly doubling of populations is possible in egg-laying facilities (48, 78). *D. gallinae* densities commonly reach up to 50,000 mites per bird in caged systems, although densities can reach 500,000 mites per bird in severe cases (57). *D. gallinae* may be present year-round, but highest densities occur during hot and humid seasons (94, 98). As the turnover of hens in laying systems often exceeds one full year (**Table 1**), such

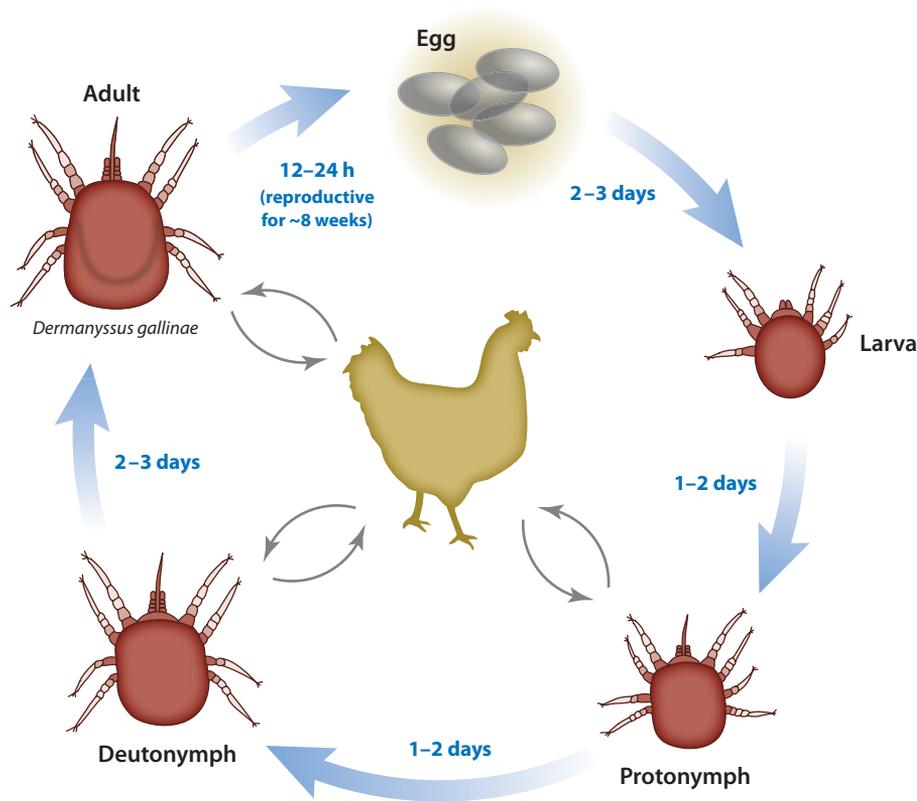


Figure 1

Life cycle of the poultry red mite, *Dermanyssus gallinae*, under favorable conditions. Eggs are laid in clutches (4–8 eggs) in refugia where larvae may remain without feeding prior to their first molt. Each female may lay up to eight clutches of eggs between feeding bouts, typically laying around 30 eggs in a lifetime. Image reproduced and adapted with permission from Maurer & Perler (80). ©FiBL (Research Institute of Organic Agriculture).

conditions are typically encountered during any production cycle, affording ample opportunity for *D. gallinae* populations to proliferate. Even when birds are removed from premises between production cycles (Table 1), *D. gallinae* may survive for long enough to infest any new flock, persisting for up to 8 months without a meal in extreme circumstances (9, 21).

Prevalence

In the United Kingdom, between 60% and 85% of commercial egg-laying facilities may be infested with *D. gallinae* (30, 41). More recent figures suggest greater variation in prevalence both in the United Kingdom and throughout Europe, with all sampled facilities infested in certain countries (18, 108) (Table 1). In Europe, the introduction of *D. gallinae* into poultry houses is considered to occur almost exclusively via the trade route (i.e., the movement of birds, egg crates, etc., between premises) (97), although elsewhere (e.g., in Brazil) infestation of flocks occurs via both trade and wild birds (104), many species of which may serve as hosts (105).

Several authors have reported higher prevalence and population numbers of *D. gallinae* in alternative egg production systems (30, 41, 48). Trends for reduced rates in conventional cages may

Table 1 Bird numbers and prevalence (% of houses/units) of *Dermanyssus gallinae* in egg-laying hen systems

Country/region (Reference)	Mean flock size ^a	Turnover (days) ^b	Empty period (days) ^b	Prevalence (%) by production system				
				Cage	Barn	Free-range	Backyard	Organic
United Kingdom	10,380	397	20	8–88	33	60	–	–
China (123)	–	–	–	64	–	–	–	–
Denmark	11,700	357	28	32	50	68	–	36
France	5,700 (noncaged) / 39,800 (caged)	337	24	72	50	56	–	80
The Netherlands	26,600	353	20	82	83	–	–	78
Italy	15,000–20,000	378	33	74	–	–	–	–
Japan	–	–	–	85	–	–	–	–
Montenegro	2,500–25,000	–	–	30–80	–	–	–	–
Morocco	–	–	–	55	–	–	90	–
Norway	1,900	–	–	23	–	–	–	–
Palestine (98)	–	–	–	31	–	–	–	–
Poland (18)	–	–	–	100	100	–	–	–
Serbia	–	–	–	90	–	–	–	–
Sweden (48)	c. 14,500 (1)	–	–	4	33	–	67	–
Transylvania (73)	–	–	–	–	–	–	90	–

Data obtained from Sparagano et al. (108) unless otherwise stated. –, data not available.

^aWhere multiple figures are provided, these represent either means from different production systems (e.g., those of France) or ranges as provided by the authors.

^bAveraged across different production systems according to data presented by (1).

reflect the presence of fewer mite refugia, making conventional cages less amenable to infestation and easier to treat should infestation occur (9). Nevertheless, because conventional cages can no longer be employed in the European Union on animal welfare grounds (EU Council Directive 1999/74/EC), they cannot be universally considered as a control option. Such systems had been heavily utilized in the European Union until their withdrawal in 2013 (108). A move away from conventional cages to systems incorporating more complex environments that appear to favor *D. gallinae* might logically increase infestation rates across the region.

Consequences of Infestation

There is a relationship between *D. gallinae* infestation and hen mortality; some reports record a tenfold increase in death rates following severe infestation (24). Although causal factors may vary, in extreme cases *D. gallinae* numbers may be so high that hens become severely anemic, with mortality resulting from exsanguination (24, 57, 125). At a sublethal level, mite feeding may result in significant stress to hens, causing an increase in circulating corticosterone and adrenaline and a decrease in β - and γ -globulins (65). Bird sleep patterns can be disrupted by the need for increased preening, and changes in head-scratching and feather-pecking behavior can also be seen during the day (57). Increases in aggressive feather-pecking and cannibalistic behaviors have been reported

Table 2 Bacterial and viral pathogens associated with *Dermanyssus gallinae*

	Pathogen	Details
Bacteria	<i>Salmonella gallinarum</i> (R)	Isolated from mites
	<i>Salmonella enteritidis</i> (R)	Transmission demonstrated
	<i>Pasteurella multocida</i> (R)	Transmission demonstrated
	<i>Chlamydia</i> spp. (23, 100)	Isolated from mites
	<i>Borrelia anserina</i> (47)	Unknown
	<i>Erysipelotbrix rhusiopathiae</i> (R)	Isolated from mites
	<i>Listeria monocytogenes</i> (R)	Isolated from mites
	<i>Coxiella burnetii</i> (R)	Transmission demonstrated
	<i>Escherichia coli</i> (E)	Isolated from mites
	<i>Staphylococcus</i> spp. (E)	Isolated from mites
	<i>Streptomyces</i> spp. (E)	Isolated from mites
Viruses	Spirochetes (R)	Transmission demonstrated
	Avian leucosis (47)	Unknown
	Newcastle disease (R)	Isolated from mites
	Fowl poxvirus (R)	Transmission demonstrated
	St. Louis encephalitis (R)	Transmission not demonstrated
	Tick-borne encephalitis (R)	Transmission not demonstrated
	Eastern equine encephalitis (R)	Transmission demonstrated
	Western equine encephalitis (R)	Transmission demonstrated
Venezuelan equine encephalitis (R)	Transmission demonstrated	

Data obtained from review (R) or experimentation (E) by Valiente Moro et al. (117) unless otherwise stated.

following infestation, as have increased feed and water intake and decreased bird condition, growth rates, and feed conversion (21, 88). Infestation can lead to declines in egg quality (through shell thinning and spotting) and egg production (21, 24).

Even relatively small mite populations that may not affect health through feeding per se may have significant impact, as *D. gallinae* may serve as a disease vector (116, 118) (**Table 2**). Although the absolute vector competence of *D. gallinae* is unconfirmed, its potential to spread disease, including to humans (see below), should not be underestimated (116). In addition to spreading disease, infestation may limit hen immunological responses to pathogens. Heavy infestations are reported to reduce antibody titers to some viral vaccines or suppress host antibody production (53, 65). Some authors postulate that mites adopt a feeding strategy that involves minimal interference or modulation of host immunity, which could support these findings (45). This same work suggests that *D. gallinae* might determine host immunocompetence via progeny survival rates (45). Whatever the reason, hens appear unable to mount a sufficiently effective immune response to *D. gallinae*, as supported by a lack of correlation between anti-*D. gallinae* immunoglobulin Y (IgY) levels and mite infestation levels (6).

CONVENTIONAL CONTROL

The tendency of *D. gallinae* to seek refugia and survive for extended periods without taking a blood meal (see above) presents a challenge to control efforts. Worldwide, *D. gallinae* has typically been controlled using synthetic acaricides (**Table 3**), with over 35 compounds tested and proposed for

Table 3 Active ingredients/chemical families of synthetic pesticides approved, not approved specifically but in widespread use, or that have been banned for use against *Dermanyssus gallinae* throughout Europe

Country	Approved for use (year of approval)	Not specifically approved, but still widely used	Banned in the European Union since 2007
United Kingdom ^a	Phoxim (2010), abermectin (2012), various pyrethroids (n/a)	Bendiocarb	Fenitrothion, carbaryl, dichlorvos, propoxur
Italy ^a	Phoxim (2010)	Amitraz, permethrin, carbaryl	
France ^a	Phoxim (2010)	–	
The Netherlands ^a	Cyfluthrin (1997), phoxim (2010)	Amitraz, various pyrethroids	
Belgium ^a	Phoxim (2010)	Various carbamates, various pyrethroids, various organophosphates ^b	
Denmark ^a	Phoxim (2010)	Propoxur, dichlorvos	
Germany	Phoxim (2010)	–	
Poland	–	Trichlorfon, dichlorvos	
Greece	Phoxim (2010)	Amitraz, carbaryl, various pyrethroids	
Sweden	Phoxim (2010)	Metrifonate, propoxur, various pyrethroids	

–, data not available.

^aCountries in which the nonsynthetic spinosad has also been approved since 2010/2011.

^bOther than the approved organophosphate phoxim.

use (e.g., organochlorines, organophosphates, pyrethrin, pyrethroids, carbamates, amitraz, and endectocides) (21). At the time of writing, relatively few products were licensed in the European Union for use against *D. gallinae*, although several unlicensed (or even banned) products were still widely employed to target infestations in this region (77, 81) (Table 3).

Resistance and Legislation

Resistance of *D. gallinae* to carbamates and pyrethroids has been widely reported and observed in the United Kingdom (30, 113), Sweden (95), France (13), and Italy (75). In a survey of British farms published in 2004, more than 60% had experienced acaricide-resistant infestations (41). Figures have likely worsened since, with problems exacerbated by product misuse in some regions (77).

In many countries the use of synthetic products is further limited as stricter legislation now exists regarding active ingredients. This has led to reduced product availability in recent years, with this trend likely to continue in the future. From the turn of the century until recently, no registered compounds were available for the control of poultry ectoparasites in Sweden (22). Similarly, no active ingredients were registered for use against *D. gallinae* in Italy between 2007 and 2010 (77), with the same appearing to be true in other European countries (Table 3). Although synthetic acaricides are still available for approved use against *D. gallinae* in the United Kingdom (Table 3), the once-popular organophosphate fenitrothion is no longer among them (30). Further constraints to conventional acaricide use include lengthy product-withdrawal periods postspraying, and restrictions preventing treatment while birds are laying (106). Such measures are typically

imposed to minimize the risks of product residues, which are reported to be a global issue (8, 77). Consumer awareness and demand for pesticide-free produce are also driving a move away from synthetics; this is true in many production sectors (87).

Product Development

Few new synthetic acaricides are being developed against *D. gallinae*. A phoxim-based product (ByeMite, Bayer, Germany) has recently been registered in the European Union (**Table 3**) and has demonstrated 97–99% efficacy in multiple systems with repeat application at 2,000 ppm (54, 84, 85). Nevertheless, the effectiveness of ByeMite against *D. gallinae* has been reported as variable, depending on the application method and geographical region (2). Indeed, resistance to phoxim is already suspected in central Poland (127).

EMERGING AND FUTURE CONTROL STRATEGIES

With increasing resistance of *D. gallinae* to synthetic acaricides and changes in legislation and production practices affecting large areas of the globe, it is likely that *D. gallinae* will pose an ever-increasing threat to global poultry production. *D. gallinae* feeds from a range of alternative hosts, including over 30 species of wild birds (105), horses (86), rodents (31, 71), and humans. Attacks on humans are not uncommon, with *D. gallinae* proposed as an occupational hazard for poultry workers (17). Outside the poultry sector, attacks have been reported in private residences, hospitals, and office spaces due to synanthropic infested birds (12, 16, 71, 102, 103).

Effective control of *D. gallinae* is therefore potentially important not only in the poultry sector, but also in numerous other sectors, human health included.

Novel Acaricides

For the purposes of this review, only nonsynthetic products qualified for inclusion as novel acaricides; synthetic products are discussed above. Two main classes of products were considered: biopesticides and plant-derived products.

Biopesticides. Toxicity of spinosad to mites has been reported as variable and/or reduced in comparison to other insect species (49), although *D. gallinae* appears susceptible both in vitro and in vivo (34, 70). Combined, these studies demonstrate at least 97% product efficacy after a single dose, with residual efficacy of at least 28 days. Since 2010, spinosad has been approved for use with laying birds in several EU countries under the product name Elector (Elanco, Greenfield, Indiana) (**Table 3**). *Bacillus thuringiensis* (*Bt*) may offer a future biopesticide option for *D. gallinae* control, with known toxicity to insects and confirmed toxicity to *O. sylviarum* (83). Nevertheless, the exotoxin thuringiensin, on which this work was based, is also toxic to vertebrates, leading several authors to advise against its use in poultry (2, 21).

Plant-derived products. Pesticides based on plant constituents are already used against pests of veterinary significance, including poultry mites (33). Topical application of Garlic Barrier (Garlic Research Labs, Glendale, California) reduced *O. sylviarum* incidence on treated hens (15) and Breck-a-Sol, a garlic-based acaricide, is recommended for use against *D. gallinae* by its developer (ECOspray, United Kingdom). A commercially available neem-based product (MiteStop, Felema, Switzerland) has shown acaricidal activity against *D. gallinae* (72), displaying greater efficacy than phoxim (2).

Precommercial research with *D. gallinae* and plant essential oils has produced some promising results (38, 59, 60, 81, 92). Such products are suggested to penetrate mite refugia, as multiple

studies have demonstrated vapor-phase toxicity (35, 59, 92). This may further promote the use of essential oils as volatile repellents, with *D. gallinae* shown to avoid odors from the oils of numerous plant species (14, 37). The repellent nature of plant products appears to be the driving force behind Red Mite Avian (Bugico S.A., Switzerland), a drinking water additive based on extracts of thyme (*Thymus* spp.), burdock (*Arctium* spp.), and tansy (*Tanacetum vulgare*) that claims to act as a deterrent to mite feeding by rendering host blood unacceptable. Scientific confirmation of this product is wanting, but reports of its commercial success (starved mites) are not uncommon (D. George, personal observation). Use of Red Mite Avian in an integrated approach may be particularly effective as starved *D. gallinae* may be more susceptible to acaricides (36).

Perhaps the greatest constraint to the use of plant-based products in *D. gallinae* control is their relative lack of standardization and consequent inconsistent efficacy (35, 52, 88). Chemical differences between seemingly similar oils can result from variations in a number of factors, including environmental conditions, harvesting regimens, and extraction protocols (35, 52). This problem might be resolved by isolating active components from plant products and developing them for use as acaricides; geraniol and several forms of cinnamaldehyde are toxic to *D. gallinae* (32, 92).

Vaccines

Vaccines provide an attractive alternative to acaricides for numerous reasons, although the development of vaccines against arthropods is notoriously difficult. This is due to the time-consuming process of identification and characterization of new protective antigens and the fact that host immune reactions can be expected to attack the arthropod in question (82, 124). The development of vaccines against *D. gallinae* is further hindered by our relatively poor understanding of the mite-host relationship (43).

Although hens can become resistant to *O. sylviarum* (26, 61), they do not appear to develop resistance to *D. gallinae* (94). Perhaps as a result, until recently there were few reports in the literature detailing the development of a prospective vaccine against *D. gallinae*. Immunization of birds with somatic *D. gallinae* antigens or homologous proteins from other mite species, e.g., *Dermatophagoides pteronyssinus* (66), has been attempted but with variable success. Significant in vitro increases in *D. gallinae* mortality (between 7.5% and 50.6%) have been achieved when mites were fed blood spiked with egg-extracted antibodies from immunized birds (43, 126). Nevertheless, no significant mortality was recorded when mites were fed in vitro blood from birds immunized with *D. gallinae* proteins (7). In vitro mite feeding/mite rearing remains imperfect, although advances in this area may facilitate future research (5, 11, 44).

An alternative approach to the use of somatic mite proteins has been the immunization of hens with recombinant proteins derived from ticks (Bm86) or mosquitoes (subolesin). In vitro mortality of *D. gallinae* was reported to be 35% and 23% in subolesin- and Bm86-immunized groups, respectively (42). A genomics approach has been undertaken to investigate vaccine candidates against *D. gallinae* using *Dg*-HRF-1 (*D. gallinae* histamine release factor protein) (an orthologue of a tick HRF that has been identified in *D. gallinae*) (11) and both *Dg*-CatD-1 and *Dg*-CatL-1 (recombinant cathepsin D- and L-like proteinases) (10). Immunization of hens with *Dg*-HRF-1 yielded a significant 7% increase in *D. gallinae* mortality when tested in vitro (using blood spiked with polyclonal IgY) (11). Similarly, mite mortality in *Dg*-CatD-1 treatment groups was significantly higher than in *Dg*-CatL-1 and control groups 120 h after initial mite feeding (10).

This antigen research has demonstrated that there is potential to develop a vaccine against *D. gallinae* based on somatic or recombinant proteins, with any vaccine likely to combine both

exposed and concealed antigens. However, significant technical hurdles still need to be overcome before a commercially viable vaccine can be recommended and released.

Biological Control

Biological control is commonly adopted in other food production sectors, although it has only recently begun to be developed for use against *D. gallinae*. Here we consider natural enemies, entomopathogenic fungi, nematodes, and bacterial endosymbionts.

Natural enemies. Augmentative biological control may be especially effective in enclosed systems where pest natural enemy dispersal is restricted. This technique might be useful for controlling *D. gallinae*, especially as several natural enemies have been suggested or used (albeit with varying success) to control other pests, particularly flies, occurring in poultry houses (9, 121).

Numerous predatory mites may be associated with poultry production and/or wild bird nests (9, 69, 121). Although not all mites have been subject to scientific scrutiny, the ability of the predatory mites *Androlaelaps casalis*, *Hypoaspis aculeifer*, *Hypoaspis miles*, and *Stratiolaelaps scimitus* to consume *D. gallinae* has been confirmed (4, 68, 69). Commercialization of biological control of *D. gallinae* has followed in recent years using these species, at least in Europe; however, additional research is still required to ensure field efficacy and consequent long-term adoption (68). Field performance may be temperature dependent and limited by alternative prey (4, 68).

It is possible that other predatory species would consume *D. gallinae*, and many have been reported as resident in poultry houses and capable of doing so (9, 21). The histereid beetle *Carcinops pumilio* is often encouraged by poultry producers, though mass rearing of this species for augmentative release may be difficult to achieve (D.R. George, personal observation). Relatively bulky beetles are perhaps also unlikely to penetrate *D. gallinae* refugia. Spatial separation of predator and prey may also limit the efficacy of predatory mites, at least for those species that tend to dwell in manure (68). Slow-release systems, which encourage gradual release of predatory mites from holding chambers and can be installed at elevated locations, have been suggested to alleviate this constraint (68), and they are already commercially available from some suppliers (e.g., Refona, Netherlands).

Entomopathogenic fungi and nematodes and bacterial endosymbionts. The use of fungi specifically against the Acari has been reviewed elsewhere, where records of 58 fungal species infecting 73 acarine species have been collated (19). *D. gallinae* is susceptible to infection by fungal isolates of *Beauveria bassiana*, *Metarhizium anisopliae*, *Trichoderma album*, and *Paecilomyces fumosoroseus* when mites were inoculated with high doses of conidia under laboratory conditions (53, 110, 112). Under semifield conditions, however, experiments typically reveal unsatisfactory control (111). Attempts to overcome reduced field efficacy by applying isolates of *M. anisopliae* at high concentration (1×10^9 conidia/ml) to caged hens have been only partly successful (112). The authors reported a significant decrease in *D. gallinae* numbers that persisted for 4 weeks posttreatment, although treatment was ineffective at a lowered dose. No work on the efficacy of nematodes for *D. gallinae* control has been published to date, but attempts to manage fly and beetle populations in poultry systems with nematodes have been similarly ineffective, despite promising in vitro results (9). Both fungi and nematodes require relatively specific environmental conditions to act (e.g., very high humidity or free water), which may limit their efficacy when deployed against *D. gallinae* in the field. Unless this requirement can be overcome somehow, effective commercial application is perhaps unlikely.

Endosymbiotic bacteria coexist with many arthropods and can be vital to host survival (129). The mycetocyte symbioses are a good example, as they are critical to numerous invertebrates that

feed on nutritionally deficient diets, blood included (28, 67). Removal of bacteria (and yeasts) that contribute to this symbiosis leads to dramatic declines in host reproduction and growth, as symbionts are irreplaceable owing to their acquisition by vertical transfer only. By disrupting oogenesis and inducing cytoplasmic incompatibility, endosymbiotic bacteria may exert further detrimental effects on host reproductive potential, as reported for members of the genera *Wolbachia* and 'Candidatus Cardinium' (40, 51). Although *Wolbachia* species have not been identified in *D. gallinae*, 'Candidatus Cardinium' and *Spiroplasma* have been recorded in these mites (25, 118). Endosymbiont targeting could contribute to the management of *D. gallinae* in the future.

Semiochemicals and Growth Regulators

As reported above, *D. gallinae* is thought to use kairomones in host location and pheromones in aggregation processes. This behavior suggests attractants could play a role in *D. gallinae* control (if used alongside acaricides in attract-and-kill schemes) or at least monitoring. Although no commercial *D. gallinae* attractant was available at the time of writing, researchers have identified mite-related aggregation pheromones (64). In this same work the authors reported evidence of host-related kairomones that could act as attractants, with independent workers identifying and patenting an additional kairomone from chickens, as well as a repellent allomone from ducks (99). Derived from the uropygial gland, a synthetic version of this duck repulsive allomone has been developed and is commercially available (Wakumo, V eto-pharma, France). An important consideration with any attractant/repellent approach is the typically volatile nature of the product used, which can result in only minimal persistence in the environment. With the recent and continuing development of a multitude of slow-release mechanisms (74), however, this property is perhaps unlikely to pose a significant constraint to current and future use of attractants and/or repellents in *D. gallinae* control.

Growth regulators (GRs) either disrupt the formation of chitin (the building block of invertebrate exoskeletons) or interfere with maturation by mimicking or inhibiting the juvenile hormone (leading to delayed or premature development of pupae or adults, respectively; 115). Although a multitude of GRs are commercially available and have been the subject of research for many years, they have been considered for use against *D. gallinae* only recently. Initial studies demonstrated the potential of triflumuron to reduce egg hatch (62), as disruption to embryonic development is an additional function of chitin inhibitors. A later study confirmed a chitin-inhibiting effect of triflumuron on *D. gallinae*, also demonstrating that efficacy could be optimized in combination with acaricides (63). Triflumuron is currently widely available for use with poultry and is marketed (at least in the United Kingdom) for general use against pests of housed domesticated animals.

Design of Premises, Hygiene, and Hazard Analysis

Removing all potential *D. gallinae* refugia from a poultry house may be unrealistic. Nevertheless, it should be possible to design facilities that are less mite friendly than is currently the norm, for example, by minimizing mite refugia and contact points with hens (88). In addition, sound hygiene practices such as regular house cleaning are generally underestimated in their potential for *D. gallinae* control (88). Cleaning with water can greatly reduce the number of mites and mite eggs present (94), although available models suggest that mechanical cleaning and sanitary clearance alone are less likely to eradicate infestations than repeat treatment with synthetic acaricides (50).

Recent research suggests that using a NASA-pioneered Hazard Analysis and Critical Control Point (HACCP) method can help prevent *D. gallinae* establishment in all types of poultry

production systems (89). Forty-one potential infestation hazards in 13 main Hazard Categories are cited with suggested corrective actions, or critical control points, for each. Hazard categories include the environment, feed, litter, equipment, visitors, and employees, among others. The HACCP method has been trialed in the Netherlands and the United Kingdom and described as a useful and feasible management tool by poultry farmers (89).

Physical Control

Although physical control may incorporate measures such as manual cleaning, here we consider temperature, lighting, and inert substances only; hygiene practices are discussed above.

Temperature. All *D. gallinae* can be expected to not survive at temperatures greater than 45°C and less than -20°C (96). Consequently, heating poultry houses between flocks to 55°C has been suggested for *D. gallinae* control, although care must be taken not to damage structures with excessive heat exposure (88). Because high mortality of *D. gallinae* occurs at 35°C (114), lower temperatures may be equally useful, especially if maintained for longer periods. Heating between flocks to 45°C and higher is commonly employed for *D. gallinae* control in Norway, perhaps as relatively small flock sizes (**Table 2**) may promote heat treatment of smaller units. When heat treatment is used in combination with chemical treatment, excellent control efficacy has been achieved; however, when used in isolation, temperature treatment of larger Dutch poultry houses has proven to be less successful (88). Raising temperatures in larger units, which are difficult to heat evenly, is also more expensive. Unsurprisingly, the economic implications of achieving and maintaining high temperatures to control *D. gallinae* remain a major constraint to the use of this technique (88).

Lighting regimen. Short-cycle intermittent light/dark periods can markedly reduce *D. gallinae* numbers, probably by disrupting the mites' normal nocturnal feeding cycle, compared with more standard regimens (109). Although *D. gallinae* may begin host-searching 1 h after the onset of darkness, most activity does not occur until 5–11 h into the dark period (79). Current EU legislation, however, requires a statutory 8-h dark period, making it difficult to envisage how intermittent lighting regimens could be employed in practice (at least in this region). Intermittent lighting could perhaps be used during normal light periods with (presumably) fewer welfare implications, but this option has not been considered. Similarly, it may be possible to use specific wavelengths to target *D. gallinae* during normal dark periods without disrupting these periods for hens. Even if such measures could be implemented, evidence suggests that any effect of lighting regimen would weaken over time, with mites willing to feed under light conditions even when unforced (88, 93). In addition, as studies are often conducted at a higher intensity of light than one would expect commercially, a reduced effect might be expected under conditions representative of poultry facilities.

Inert substances. Inert substances include primarily DE (diatomaceous earth), kaolin, and silicas. Many exist as fine-particle powders, though issues with application and dust formation are driving forward liquid formulations (81, 91). Many standard products are already available commercially and widely used (e.g., InsectoSec, BIOFA, Germany, and Decimite+, BASF, Germany). As with all such products, they absorb lipids from the surface of mites (120), effectively leading to death by dehydration.

Work with *D. gallinae* and inert substances has shown that efficacy can be greatly affected by the quality of the raw material used (58, 81). High humidity levels (>85%) reduce efficacy, suggesting that when these products are used in poultry units, increased application rates may be necessary

(58). Work with *O. sylviarum* supports the limitations of DE and kaolin as acaricides, in which neither was as effective as other nontraditional acaricides tested (although kaolin provided control for 2–3 weeks following repeat application to birds) (91).

In some cases DE products are also supplied mixed with other active ingredients. The combined use of plant-based products and DE is increasingly popular (D.R. George, personal observation); several products based on this combination (e.g., MPoux, Olmix, France) are commercially available.

INTEGRATED PEST MANAGEMENT POTENTIAL

Integrated pest management (IPM) is well established in other production sectors, and recommended combined treatment regimens for poultry pests, including *D. gallinae*, date back many years (9, 20). Today, poultry producers often implement some form of biosecurity in conjunction with multifaceted treatment programs involving cleaning/disinfecting and the use of physical agents and synthetic acaricides (81). Compared with other sectors, however, comprehensive IPM remains relatively rare in the poultry industry; the full potential of this technique for *D. gallinae* control is perhaps unrealized as a result (46, 88).

Of the varied *D. gallinae* management approaches that have been reviewed here, many would be amenable to integration. Should a vaccine against *D. gallinae* become available, it likely could be used in conjunction with any other control method, similar to HACCP analysis. Similarly, the efficacy of novel pesticides, inert products, semiochemicals, and GRs would be unaffected (and perhaps even improved) by advances in animal/premise husbandry techniques, as all these would be compatible with one another as well as with conventional *D. gallinae* control. Such compatibility would not necessarily imply benefit (81), however, and would not be universal for all the management options considered. Broad-spectrum approaches, such as the use of some novel pesticides, inert dusts, GRs, and heat treatment, would likely have an adverse effect on natural enemies and biological control. Although this effect may limit their use in IPM, they could be employed to target multiple invertebrate pests with a single application, as shown by MiteStop (3, 122) and some essential oils (39). Much remains to be done to promote comprehensive IPM for *D. gallinae* and to devise optimal treatment regimens, of which the latter has seen the least progress in the past 10–15 years. Recent advances in *D. gallinae* population modeling (50), coupled with empirical research, should facilitate work in this area, revealing optimal IPM strategies for immediate and future use.

CONCLUSIONS

D. gallinae is a serious threat to laying hens and egg production in many parts of the world, and acaricide resistance and changes in pesticide and hen welfare legislation are set to exacerbate this issue in many countries. As the role of *D. gallinae* as a disease vector becomes better understood, its pest status increases commensurately. Recent reports of *D. gallinae* infestations in a range of alternative hosts further contribute to this status. Should existing trends continue, *D. gallinae* could soon be problematic for other domestic fowl, pets, and even humans, as it is for poultry.

The recent increase in *D. gallinae*-related research has improved our understanding of this pest's biology and ecology, prompting investigation into control through pheromones, hazard analysis, premise hygiene, and heat treatment. Advances in microbiology and in vitro rearing techniques continue to facilitate the search for an effective vaccine against *D. gallinae*, and past successes in other areas of pest management have informed the development of plant-derived

TARGETING *D. GALLINAE* ACARICIDE RESISTANCE

In addition to developing novel acaricides and management interventions in response to pest resistance, it may be possible to target the metabolic pathways that confer resistance to begin with. Arthropods' detoxification of pesticides could rely on several enzyme families such as the glutathione *S*-transferases, esterases (or carboxylesterases) and cytochrome P450s. It may be possible to target and inhibit these enzymes to effectively break pest resistance mechanisms, prolonging or even restoring the effectiveness of existing pesticides. The staggering diversity of potential detoxifying enzymes currently represents a limiting step in this novel and potentially exciting approach, making identification of precisely which enzymes confer resistance problematic. Nevertheless, continuing research in this field, including with *D. gallinae*, could lead to significant breakthroughs in pest resistance management in the not-too-distant future, permitting improvements to existing pesticide synergists such as piperonyl butoxide (a generalist P450 inhibitor). Recent advances in the sequencing of acarine genomes (e.g., *Tetranychus urticae*, and the soon-to-be-released *Ixodes scapularis*) could further facilitate the identification of relevant detoxification pathways in this group at the genetic level (130, 131).

products, natural enemies, growth regulators, and biopesticides. Many of these approaches, whether they are experimental, near-market, or commercial, appear amenable to combination with one another in an IPM approach. Although such integration will not automatically guarantee benefit, investigation of its full potential in *D. gallinae* control is recommended nonetheless.

Development of more comprehensive IPM regimens for *D. gallinae* should be facilitated by ongoing developments in monitoring and modeling of populations, with these being key areas for future research to promote optimally efficient deployment of any control program. Confirming the threat posed by *D. gallinae* to nonavian hosts is also an important objective deserving more attention and is furthered by recent advances in our understanding of this mite's phylogeny and improved access to online keys to aid taxonomy. Finally, if a role for current and future synthetic acaricide use in *D. gallinae* control is accepted, significant benefit could be realized through continued research into targeting acaricide resistance mechanisms in this species (see sidebar, Targeting *D. gallinae* Acaricide Resistance).

SUMMARY POINTS

1. *D. gallinae* remains a serious threat to laying hens and egg production in many parts of the world.
2. Acaricide resistance and changes in pesticide and hen welfare legislation may exacerbate future management of *D. gallinae* in many countries.
3. *D. gallinae* may serve as a disease vector, but the full extent of its vector capacity remains unknown.
4. Recent reports of infestations in a range of alternative hosts increasingly suggest that *D. gallinae* may survive, or at least feed, on hosts other than birds.
5. Since the last major review on *D. gallinae*, research effort devoted to understanding and controlling this pest has increased.

6. Particular progress has been made in fields related to behavior, etiology, and physiology (e.g., semiochemicals, hazard analysis, premise hygiene, and heat treatment), microbiology (e.g., in vitro rearing and associated vaccine development), novel acaricides (e.g., biopesticides, plant-derived products, and growth regulators), and biological control.
7. Many of these areas (e.g., vaccine development) require further investigation before research can be translated into commercial practice; however, options currently available for *D. gallinae* control are varied and increasing.
8. Comprehensive IPM programs for *D. gallinae* control are rare, though such programs could be of use in managing this pest in the future.

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LITERATURE CITED

1. Agra CEAS Consult. Ltd. 2004. Study on the socio-economic implications of the various systems to keep laying hens. In *Final Report for the European Commission*. Kent, UK: Agra CEAS Consult. Ltd.
2. Abdel-Ghaffar F, Semmler M, Al-Rasheid K, Mehlhorn H. 2009. In vitro efficacy of ByeMite and Mite-Stop on developmental stages of the red chicken mite *Dermanyssus gallinae*. *Parasitol. Res.* 105:1469–71
3. Al-Quraishy S, Abdel-Ghaffar F, Al-Rasheid KAS, Mehlhorn J, Mehlhorn H. 2012. Effects of a neem seed extract (MiteStop®) on mallophages (featherlings) of chicken: in vivo and in vitro studies. *Parasitol. Res.* 110:617–22
4. Ali W, George DR, Shiel RS, Sparagano OA, Guy JH. 2012. Laboratory screening of potential predators of the poultry red mite (*Dermanyssus gallinae*) and assessment of *Hypoaspis miles* performance under varying biotic and abiotic conditions. *Vet. Parasitol.* 187:341–44
5. Arkle S, George DR, Guy JH, Sparagano OA. 2010. Comparison of in vivo and in vitro survival and fecundity rates of the poultry red mite, *Dermanyssus gallinae*. *Res. Vet. Sci.* 88:279–80
6. Arkle S, Guy JH, Sparagano O. 2006. Immunological effects and productivity variation of red mite (*Dermanyssus gallinae*) on laying hens: implications for egg production and quality. *World Poult. Sci. J.* 62:249–57
7. Arkle S, Harrington D, De Luna C, George D, Guy J, Sparagano OA. 2009. Immunological control of poultry red mite: the use of whole mite antigens as a candidate vaccine. *Ann. N.Y. Acad. Sci.* 1149:36–40
8. Aulakh RS, Gill JPS, Bedi JS, Sharma JK, Joia BS, Ockerman HW. 2006. Organochlorine pesticide residues in poultry feed, chicken muscle and eggs at a poultry farm in Punjab, India. *J. Sci. Food Agric.* 86:741–44
9. Axtell RC. 1999. Poultry integrated pest management; status and future. *Integr. Pest Manag. Rev.* 4:53–73

10. Bartley K, Huntley JF, Wright HW, Nath M, Nisbet AJ. 2012. Assessment of cathepsin D and L-like proteinases of poultry red mite, *Dermanyssus gallinae* (De Geer), as potential vaccine antigens. *Parasitology* 139:755–65
11. Bartley K, Nisbet AJ, Offer JE, Sparks NHC, Wright HW, Huntley JF. 2009. Histamine release factor from *Dermanyssus gallinae* (De Geer): characterization and in vitro assessment as a protective antigen. *Int. J. Parasitol.* 39:447–56
12. Bellanger AP, Bories C, Foulet F, Bretagne S, Botterel F. 2008. Nosocomial dermatitis caused by *Dermanyssus gallinae*. *Infect. Control Hosp. Epidemiol.* 29:282–83
13. **Beugnet F, Chauve C, Gauthey M, Beert L. 1997. Resistance of the red poultry mite to pyrethroids in France. *Vet. Rec.* 140:577–79**
14. Birkett MA, Hassanali A, Høglund S, Pettersson J, Pickett JA. 2011. Repellent activity of catmint, *Nepeta cataria*, and iridoid nepetalactone isomers against Afro-tropical mosquitoes, ixodid ticks and red poultry mites. *Phytochemistry* 72:109–14
15. Birrenkott GP, Brockenfelt GE, Greer JA, Owens MD. 2000. Topical application of garlic reduces northern fowl mite infestation in laying hens. *Poult. Sci.* 79:1575–77
16. Cafiero MA, Camarda A, Circella E, Santagada G, Schino G, Lomuto M. 2008. Pseudoscabies caused by *Dermanyssus gallinae* in Italian city dwellers: a new setting for an old dermatitis. *J. Eur. Acad. Dermatol. Venereol.* 22:1382–83
17. Cafiero MA, Galante D, Camarda A, Giangaspero A, Sparagano O. 2011. Why dermanyssosis should be listed as an occupational hazard. *Occup. Environ. Med.* 68:628
18. Cencek T. 2003. Prevalence of *Dermanyssus gallinae* in poultry farms in Silesia Region in Poland. *Bull. Vet. Inst. Pulawy* 47:465–69
19. Chandler D, Davidson G, Pell JK, Ball BV, Shaw K, Sunderland KD. 2000. Fungal biocontrol of Acari. *Biocontrol Sci. Technol.* 10:357–84
20. Chatterton P. 2000. Rotational control programme for poultry red mite. *Int. Pest Control* 42:84–85
21. **Chauve C. 1998. The poultry red mite *Dermanyssus gallinae* (De Geer, 1778): current situation and future prospects for control. *Vet. Parasitol.* 79:239–45**
22. Chirico J, Tauson R. 2002. Traps containing acaricides for the control of *Dermanyssus gallinae*. *Vet. Parasitol.* 110:109–16
23. Circella E, Pugliese N, Todisco G, Cafiero MA, Sparagano OA, Camarda A. 2011. *Cblamydia psittaci* infection in canaries heavily infested by *Dermanyssus gallinae*. *Exp. Appl. Acarol.* 55:329–38
24. Cosoroaba I. 2001. Massive *Dermanyssus gallinae* invasion in battery-husbandry raised fowls. *Rev. Med. Vet. Toulouse* 152:89–96
25. De Luna CJ, Moro CV, Guy JH, Zenner L, Sparagano OA. 2009. Endosymbiotic bacteria living inside the poultry red mite (*Dermanyssus gallinae*). *Exp. Appl. Acarol.* 48:105–13
26. DeVaney JA, Ziprin RL. 1980. Acquired immune response of white leghorn hens to populations of northern fowl mite, *Ornithonyssus sylviarum* (Canestrini and Fanzago). *Poult. Sci.* 59:1742–44
27. **Di Palma A, Giangaspero A, Cafiero MA, Germinara GS. 2012. A gallery of the key characters to ease identification of *Dermanyssus gallinae* (Acari: Gamasida: Dermanyssidae) and allow differentiation from *Ornithonyssus sylviarum* (Acari: Gamasida: Macronyssidae). *Parasites Vectors* 5:104**
28. Douglas AE. 2007. Symbiotic microorganisms: untapped resources for insect pest control. *Trends Biotechnol.* 25:338–42
29. Entrekin DL, Oliver JH Jr. 1982. Aggregation of the chicken mite, *Dermanyssus gallinae* (Acari: Dermanyssidae). *J. Med. Entomol.* 19:671–78
30. Fiddes MD, Le Gresley S, Parsons DG, Epe C, Coles GC, Stafford KA. 2005. Prevalence of the poultry red mite (*Dermanyssus gallinae*) in England. *Vet. Rec.* 157:233–35
31. Gaaboub IA, Donia AH, Kelada NL, Abdelkarim MEH. 1982. Ectoparasites of some rodents from the edge of the Western Desert near Alexandria, Egypt. *Insect Sci. Appl.* 3:145–50
32. George DR, Biron JM, Jolly G, Duvallet G, Sparagano OAE. 2009. Toxicity of geraniol solution in vitro to the poultry red mite, *Dermanyssus gallinae*. *Parasite* 16:319–21
33. George DR, Guy JH, Arkle S, Harrington D, De Luna C, et al. 2008. Use of plant-derived products to control arthropods of veterinary importance: a review. *Ann. N.Y. Acad. Sci.* 1149:23–26
13. Gives first report of *Dermanyssus gallinae* developing resistance to pyrethroids.
21. Is the last major review in a leading journal solely devoted to *Dermanyssus gallinae* and its control.
27. Provides the first open-access, easily accessible key to *Dermanyssus gallinae*.

34. George DR, Shiel RS, Appleby WG, Knox A, Guy JH. 2010. In vitro and in vivo acaricidal activity and residual toxicity of spinosad to the poultry red mite, *Dermanyssus gallinae*. *Vet. Parasitol.* 173:307–16
35. George DR, Smith TJ, Shiel RS, Sparagano OA, Guy JH. 2009. Mode of action and variability in efficacy of plant essential oils showing toxicity against the poultry red mite, *Dermanyssus gallinae*. *Vet. Parasitol.* 161:276–82
36. George DR, Smith TJ, Sparagano OAE, Guy JH. 2008. The influence of ‘time since last blood meal’ on the toxicity of essential oils to the poultry red mite (*Dermanyssus gallinae*). *Vet. Parasitol.* 155:333–35
37. George DR, Sparagano OA, Port G, Okello E, Shiel RS, Guy JH. 2009. Repellence of plant essential oils to *Dermanyssus gallinae* and toxicity to the non-target invertebrate *Tenebrio molitor*. *Vet. Parasitol.* 162:129–34
38. George DR, Sparagano OA, Port G, Okello E, Shiel RS, Guy JH. 2010. Environmental interactions with the toxicity of plant essential oils to the poultry red mite *Dermanyssus gallinae*. *Med. Vet. Entomol.* 24:1–8
39. George DR, Sparagano OA, Port G, Okello E, Shiel RS, Guy JH. 2010. Toxicity of plant essential oils to different life stages of the poultry red mite, *Dermanyssus gallinae*, and non-target invertebrates. *Med. Vet. Entomol.* 24:9–15
40. Gotoh T, Sugawara J, Noda H, Kitashima Y. 2007. *Wolbachia*-induced cytoplasmic incompatibility in Japanese populations of *Tetranychus urticae* (Acari: Tetranychidae). *Exp. Appl. Acarol.* 42:1–16
41. Guy JH, Khajavi M, Hlalel MM, Sparagano O. 2004. Red mite (*Dermanyssus gallinae*) prevalence in laying units in northern England. *Br. Poult. Sci.* 45 (Suppl.):5–6
42. Harrington D, Canales M, de la Fuente J, de Luna C, Robinson K, et al. 2009. Immunisation with recombinant proteins subolesin and Bm86 for the control of *Dermanyssus gallinae* in poultry. *Vaccine* 27:4056–63
43. Harrington D, Din HM, Guy J, Robinson K, Sparagano O. 2009. Characterization of the immune response of domestic fowl following immunization with proteins extracted from *Dermanyssus gallinae*. *Vet. Parasitol.* 160:285–94
44. Harrington DW, Guy JH, Robinson K, Sparagano OA. 2010. Comparison of synthetic membranes in the development of an in vitro feeding system for *Dermanyssus gallinae*. *Bull. Entomol. Res.* 100:127–32
45. Harrington DW, Robinson K, Sparagano OA. 2010. Immune responses of the domestic fowl to *Dermanyssus gallinae* under laboratory conditions. *Parasitol. Res.* 106:1425–34
46. Harrington DWJ, George DR, Guy JH, Sparagano OAE. 2011. Opportunities for integrated pest management to control the poultry red mite, *Dermanyssus gallinae*. *World. Poult. Sci. J.* 67:83–93
47. Hoffmann G. 1987. Vogelmilben als Lästlinge, Krankheitserzeuger und Vektoren bei Mensch und Nutztier. *Dtsch. Tierärztl. Wschr.* 95:7–10
48. Hoglund J, Nordenfors H, Uggla A. 1995. Prevalence of the poultry red mite, *Dermanyssus gallinae*, in different types of production systems for egg layers in Sweden. *Poult. Sci.* 74:1793–98
49. Holt KM, Opit GP, Nechols JR, Margolies DC. 2006. Testing for non-target effects of spinosad on twospotted spider mites and their predator *Phytoseiulus persimilis* under greenhouse conditions. *Exp. Appl. Acarol.* 38:141–49
50. Huber K, Zenner L, Bicout DJ. 2011. Modelling population dynamics and response to management options in the poultry red mite *Dermanyssus gallinae* (Acari: Dermanyssidae). *Vet. Parasitol.* 176:65–73
51. Hunter MS, Perlman SJ, Kelly SE. 2003. A bacterial symbiont in the Bacteroidetes includes cytoplasmic incompatibility in the parasitoid wasp *Encarsia pergandiella*. *Proc. R. Soc. B* 270:2185–90
52. Isman MB. 2006. Botanical insecticides, deterrents, and repellents in modern agriculture and an increasingly regulated world. *Annu. Rev. Entomol.* 51:45–66
53. Kaoud HA. 2010. Susceptibility of poultry red mites to entomopathogens. *Int. J. Poult. Sci.* 9:259–63
54. Keïta A, Pagot E, Pommier P, Baduel L, Heine J. 2006. Efficacy of phoxim 50% E.C. (ByeMite) for treatment of *Dermanyssus gallinae* in laying hens under field conditions. *Rev. Med. Vet. Toulouse* 157:590–94
55. Kilpinen O. 2005. How to obtain a bloodmeal without being eaten by a host: the case of poultry red mite, *Dermanyssus gallinae*. *Physiol. Entomol.* 30:232–40

50. Provides the first comprehensive attempt to model *Dermanyssus gallinae* population responses to treatment.

56. Kilpinen O, Mullens BA. 2004. Effect of food deprivation on response of the mite, *Dermanyssus gallinae*, to heat. *Med. Vet. Entomol.* 18:368–71
57. Kilpinen O, Roepstorff A, Permin A, Norgaard-Nielsen G, Lawson LG, Simonsen HB. 2005. Influence of *Dermanyssus gallinae* and *Ascaridia galli* infections on behaviour and health of laying hens (*Gallus gallus domesticus*). *Br. Poult. Sci.* 46:26–34
58. Kilpinen O, Steenberg T. 2009. Inert dusts and their effects on the poultry red mite (*Dermanyssus gallinae*). *Exp. Appl. Acarol.* 48:51–62
59. Kim SI, Na YE, Yi JH, Kim BS, Ahn YJ. 2007. Contact and fumigant toxicity of Oriental medicinal plant extracts against *Dermanyssus gallinae* (Acari: Dermanyssidae). *Vet. Parasitol.* 145:377–82
60. Kim SI, Yi JH, Tak JH, Ahn YJ. 2004. Acaricidal activity of plant essential oils against *Dermanyssus gallinae* (Acari: Dermanyssidae). *Vet. Parasitol.* 120:297–304
61. Kirkwood A. 1963. Longevity of the mites *Dermanyssus gallinae* and *Liponyssus sylviarum*. *Exp. Parasitol.* 14:358–66
62. Kočíšová A, Letková V, Mitrová M. 2006. The observation of triflumuron (Baycidal 25 WP) effects on the poultry red mite (*Dermanyssus gallinae*) under practical conditions. *Proc. ICOPA, 11th, Glasgow, Abstr.* 1359
63. Kočíšová A, Plachý J. 2008. Novel approach to controlling the poultry red mite (Acarina: Mesostigmata). In *Proc. Int. Conf. Urban Pests, 6th, Budapest*, July 13–16, pp. 349–54. Hungary: OOK-Press Kft
64. Koenraad CJ, Dicke M. 2010. The role of volatiles in aggregation and host-seeking of the haematophagous poultry red mite *Dermanyssus gallinae* (Acari: Dermanyssidae). *Exp. Appl. Acarol.* 50:191–99
65. Kowalski A, Sokol R. 2009. Influence of *Dermanyssus gallinae* (poultry red mite) invasion on the plasma levels of corticosterone, catecholamines and proteins in layer hens. *Pol. J. Vet. Sci.* 12:231–35
66. Lee S, Kim J, Jee C. 2002. Immune effects on the somatic antigens against *Dermanyssus gallinae* and *Dermatophagoides pteronyssinus* in chicken. *Kor. J. Vet. Res.* 42:253–60
67. Lehane M. 2005. Managing the blood meal. In *The Biology of Blood-Sucking in Insects*, ed. M Lehane, pp. 84–115. Cambridge, UK: Cambridge Univ. Press
68. Lesna I, Sabelis MW, van Niekerk TG, Komdeur J. 2012. Laboratory tests for controlling poultry red mites (*Dermanyssus gallinae*) with predatory mites in small ‘laying hen’ cages. *Exp. Appl. Acarol.* 58:371–83
69. Lesna I, Wolfs P, Faraji F, Roy L, Komdeur J, Sabelis MW. 2009. Candidate predators for biological control of the poultry red mite *Dermanyssus gallinae*. *Exp. Appl. Acarol.* 48:63–80
70. Liebisch G, Hack R, Smid G. 2011. Efficacy of spinosad against the poultry red mite, *Dermanyssus gallinae* (Mesostigmata: Dermanyssidae), in laboratory and field trials. *Zoosymposia* 6:282–87
71. Lucky AW, Sayers C, Argus JD, Lucky A. 2001. Avian mite bites acquired from a new source—pet gerbils: report of two cases and review of the literature. *Arch. Dermatol.* 137:167–70
72. Lundh J, Wiktelius D, Chirico J. 2005. Azadirachtin-impregnated traps for the control of *Dermanyssus gallinae*. *Vet. Parasitol.* 130:337–42
73. Magdaş C, Baciú H, Mureşan A. 2004. Epidemiology of *Dermanyssus gallinae* infestation in poultry, from three Transylvanian localities. *Sci. Parasitol.* 5:65–70
74. Maia MF, Moore SJ. 2011. Plant-based insect repellents: a review of their efficacy, development and testing. *Malar. J.* 10:S11; doi: 10.1186/1475-2875-10-S1-S11
75. Marangi M, Cafiero MA, Capelli G, Camarda A, Sparagano OAE, Giangaspero A. 2009. Evaluation of the poultry red mite, *Dermanyssus gallinae* (Acari: Dermanyssidae), susceptibility to some acaricides in field populations from Italy. *Exp. Appl. Acarol.* 48: 11–18
76. Marangi M, de Luna CJ, Cafiero MA, Camarda A, le Bouquin S, et al. 2009. Phylogenetic relationship between *Dermanyssus gallinae* populations in European countries based on mitochondrial COI gene sequences. *Exp. Appl. Acarol.* 48:143–55
77. Marangi M, Morelli V, Pati S, Camarda A, Cafiero MA, Giangaspero A. 2012. Acaricide residues in laying hens naturally infested by red mite *Dermanyssus gallinae*. *PLoS One* 7:e31795
78. Maurer V, Baumgartner J. 1992. Temperature influence on life table statistics of the chicken mite *Dermanyssus gallinae* (Acari: Dermanyssidae). *Exp. Appl. Acarol.* 15:27–40
79. Maurer V, Bieri M, Fölsch DW. 1988. Das Suchverhalten von *Dermanyssus gallinae* in Hühnerställen. *Arch. Geflügelk.* 52:209–15

80. Maurer V, Perler E. 2006. Silicas for control of the poultry red mite *Dermanyssus gallinae*. *Proc. European Joint Organic Congress, Odense, May 30–31*, pp. 504–5
81. Maurer V, Perler E, Heckendorn F. 2009. In vitro effects of oils, silicas and plant preparations against the poultry red mite *Dermanyssus gallinae*. *Exp. Appl. Acarol.* 48:31–41
82. McDevitt R, Nisbet AJ, Huntley JF. 2006. Ability of a proteinase inhibitor mixture to kill poultry red mite, *Dermanyssus gallinae*, in an in vitro feeding system. *Vet. Parasitol.* 141:380–85
83. McKeen WD, Mullens BA, Rodriguez JL, Mandeville JD. 1988. *Bacillus thuringiensis* exotoxin for northern fowl mite control. *Proc. West. Poult. Dis. Conf., 47th, Sacramento, March 8–10*, pp. 140–41
84. Meyer-Kühling B, Heine J, Müller-Lindloff J, Pfister K. 2007. Epidemiology of *Dermanyssus gallinae* and acaricidal efficacy of phoxim 50% in alternative housing systems during the laying period of hens. *Parasitol. Res.* 101 (Suppl.):1–12
85. Meyer-Kühling B, Pfister K, Müller-Lindloff J, Heine J. 2007. Field efficacy of phoxim 50% (ByeMite) against the poultry red mite *Dermanyssus gallinae* in battery cages stocked with laying hens. *Vet. Parasitol.* 147:289–96
86. Mignon B, Losson B. 2008. Dermatitis in a horse associated with the poultry mite (*Dermanyssus gallinae*). *Vet. Dermatol.* 19:38–43
87. Moser R, Raffaelli R, Thilmany-McFadden D. 2011. Consumer preferences for fruit and vegetables with credence-based attributes: a review. *Int. Food Agribus. Man.* 14:121–41
88. Mul M, van Niekerk T, Chirico J, Maurer V, Kilpinen O, et al. 2009. Control methods for *Dermanyssus gallinae* in systems for laying hens: results of an international seminar. *World. Poult. Sci. J.* 65:589–99
89. Mul MF, Koenraadt CJM. 2009. Preventing introduction and spread of *Dermanyssus gallinae* in poultry facilities using the HACCP method. *Exp. Appl. Acarol.* 48:167–81
90. Mullen GR, O'Connor BM. 2009. Mites (Acari). In *Medical and Veterinary Entomology*, ed. Mullen GR, LA Durden, pp. 433–92. San Diego, CA: Academic. 2nd ed.
91. Mullens BA, Soto D, Martin CD, Callahan BL, Gerry AC. 2012. Northern fowl mite (*Ornithonyssus sylviarum*) control evaluations using liquid formulations of diatomaceous earth, kaolin, sulfur, azadirachtin, and *Beauveria bassiana* on caged laying hens. *J. Appl. Poult. Res.* 21:111–16
92. Na YE, Kim SI, Bang HS, Kim BS, Ahn YJ. 2011. Fumigant toxicity of cassia and cinnamon oils and cinnamaldehyde and structurally related compounds to *Dermanyssus gallinae* (Acari: Dermanyssidae). *Vet. Parasitol.* 178:324–29
93. Nakamae H, Fujisaki K, Kishi S, Yashiro M, Oshiro S, Furuta K. 1997. The new parasitic ecology of chicken mites *Dermanyssus gallinae*, parasitizing and propagating on chickens even in the daytime. *J. Poult. Sci.* 34:110–16
94. Nordenfors H, Höglund J. 2000. Long term dynamics of *Dermanyssus gallinae* in relation to mite control measures in aviary systems for layers. *Br. Poult. Sci.* 41:533–40
95. Nordenfors H, Höglund J, Tauson R, Chirico J. 2001. Effects of permethrin impregnated plastic strips on *Dermanyssus gallinae* in loose housing systems for laying hens. *Vet. Parasitol.* 102:121–31
96. Nordenfors H, Höglund J, Uggla A. 1999. Effects of temperature and humidity on oviposition, molting, and longevity of *Dermanyssus gallinae* (Acari: Dermanyssidae). *J. Med. Entomol.* 36:68–72
97. Oines O, Brannstrom S. 2011. Molecular investigations of cytochrome *c* oxidase subunit I (COI) and the internal transcribed spacer (ITS) in the poultry red mite, *Dermanyssus gallinae*, in northern Europe and implications for its transmission between laying poultry farms. *Med. Vet. Entomol.* 25:402–12
98. Othman RA, Abdallah JM, Abo-Omar J. 2012. Prevalence of the red mite (*Dermanyssus gallinae*) in layer flocks in four districts in northern West Bank, Palestine. *Open J. Anim. Sci.* 2:106–9
99. Pageat P. 2005. Allomone repulsive and kairomone attractive compositions for controlling arachnids. *US Patent No. 20050137119 A1*
100. Permin A, Hansen JW. 1998. Epidemiology, diagnosis and control of poultry parasites. *FAO Anim. Health Man. No. 4*. Rome: FAO
101. Potenza L, Cafiero MA, Camarda A, La Salandra G, Cucchiari L, Dacha M. 2009. Characterization of *Dermanyssus gallinae* (Acarina: Dermanyssidae) by sequence analysis of the ribosomal internal transcribed spacer regions. *Vet. Res. Commun.* 33:611–18
102. Regan AM, Metersky ML, Craven DE. 1987. Nosocomial dermatitis and pruritus caused by a pigeon mite infestation. *Arch. Intern. Med.* 147:2185–87

103. Rosen S, Yeruham I, Braverman Y. 2002. Dermatitis in humans associated with the mites *Pyemotes tritici*, *Dermanyssus gallinae*, *Ornithonyssus bacoti* and *Androlaelaps casalis* in Israel. *Med. Vet. Entomol.* 16:442–44
104. Roy L, Buronfosse T. 2011. Using mitochondrial and nuclear sequence data for disentangling population structure in complex pest species: a case study with *Dermanyssus gallinae*. *PLoS One* 6:e22305
105. Roy L, Chauve CM. 2007. Historical review of the genus *Dermanyssus* Duges, 1834 (Acari: Mesostigmata: Dermanyssidae). *Parasite* 14:87–100
106. Roy L, Chauve C, Delaporte J, Inizan G, Buronfosse T. 2009. Exploration of the susceptibility of AChE from the poultry red mite *Dermanyssus gallinae* (Acari: Mesostigmata) to organophosphates in field isolates from France. *Exp. Appl. Acarol.* 48:19–30
107. Roy L, Dowling APG, Chauve CM, Buronfosse T. 2009. Delimiting species boundaries within *Dermanyssus* Duges, 1834 (Acari: Dermanyssidae) using a total evidence approach. *Mol. Phylogenet. Evol.* 50:446–70
108. Sparagano O, Pavlicevic A, Murano T, Camarda A, Sahibi H, et al. 2009. Prevalence and key figures for the poultry red mite *Dermanyssus gallinae* infections in poultry farm systems. *Exp. Appl. Acarol.* 48:3–10
109. Stafford KA, Lewis PD, Coles GC. 2006. Preliminary study of intermittent lighting regimes for red mite (*Dermanyssus gallinae*) control in poultry houses. *Vet. Rec.* 158:762–63
110. Steenberg T, Kilpinen O. 2003. Fungus infection of the chicken mite *Dermanyssus gallinae*. *IOBC WPRS Bull.* 26:23–26
111. Steenberg T, Kilpinen O, Moore D. 2006. Fungi for control of the poultry red mite, *Dermanyssus gallinae*. *Proc. Int. Workshop Implement. Biocontrol Pract. Temp. Reg.—Present and Near Future, Flakkebjerg*, Nov. 1–3, 2005. DIAS Rep. 119, pp. 71–74
112. Tavassoli M, Allymehr M, Pourseyed SH, Ownag A, Bernousi I, et al. 2011. Field bioassay of *Metarhizium anisopliae* strains to control the poultry red mite *Dermanyssus gallinae*. *Vet. Parasitol.* 178:374–78
113. Thind BB, Ford HL. 2007. Assessment of susceptibility of the poultry red mite *Dermanyssus gallinae* (Acari: Dermanyssidae) to some acaricides using an adapted filter paper based bioassay. *Vet. Parasitol.* 144:344–48
114. Tucci EC, Prado AP, Araújo RP. 2008. Development of *Dermanyssus gallinae* (Acari: Dermanyssidae) at different temperatures. *Vet. Parasitol.* 155:127–32
115. Tunaz H, Uygun N. 2004. Insect growth regulators for insect pest control. *Turk. J. Agric. For.* 28:377–87
116. Valiente Moro C, Chauve C, Zenner L. 2005. Vectorial role of some dermanyssoid mites (Acari, Mesostigmata, Dermanyssoidea). *Parasite* 12:99–109
117. Valiente Moro C, De Luna CJ, Tod A, Guy JH, Sparagano OA, Zenner L. 2009. The poultry red mite (*Dermanyssus gallinae*): a potential vector of pathogenic agents. *Exp. Appl. Acarol.* 48:93–104
118. Valiente Moro C, Thioulouse J, Chauve C, Normand P, Zenner L. 2009. Bacterial taxa associated with the hematophagous mite *Dermanyssus gallinae* detected by 16S rRNA PCR amplification and TTGE fingerprinting. *Res. Microbiol.* 160:63–70
119. van Emous R. 2005. Wage war against the red mite! *Poult. Int.* 44: 26–33
120. Vincent C, Hallman G, Panneton B, Fleurat-Lessard F. 2003. Management of agricultural insects with physical control methods. *Annu. Rev. Entomol.* 48:261–81
121. Wales AD, Carrique-Mas JJ, Rankin M, Bell B, Thind BB, Davies RH. 2010. Review of the carriage of zoonotic bacteria by arthropods, with special reference to *Salmonella* in mites, flies and litter beetles. *Zoonoses Public Health* 57:299–314
122. Walldorf V, Mehlhorn H, Al-Quraishy S, Al-Rasheid KA, Abdel-Ghaffar F, Mehlhorn J. 2012. Treatment with a neem seed extract (MiteStop®) of beetle larvae parasitizing the plumage of poultry. *Parasitol. Res.* 110:623–27
123. Wang FF, Wang M, Xu FR, Liang DM, Pan BL. 2010. Survey of prevalence and control of ectoparasites in caged poultry in China. *Vet. Rec.* 167:934–37
124. Willadsen P. 2004. Anti-tick vaccines. *Parasitology* 129 (Suppl.):S367–87
125. Wojcik AR, Grygon-Frankiewicz B, Zbikowska E, Wasielewski L. 2000. Invasion of *Dermanyssus gallinae* (De Geer, 1778) in poultry farms in the Torun region. *Wiad. Parazytol.* 46:511–15
126. Wright HW, Bartley K, Nisbet AJ, McDevitt RM, Sparks NHC, et al. 2009. The testing of antibodies raised against poultry red mite antigens in an in vitro feeding assay: preliminary screen for vaccine candidates. *Exp. Appl. Acarol.* 48:81–91

127. Zdybel J, Karamon J, Cencek T. 2011. In vitro effectiveness of selected acaricides against red poultry mites (*Dermanyssus gallinae*, De Geer, 1778) isolated from laying hen battery cage farms localised in different regions of Poland. *Bull. Vet. Inst. Pulawy* 55:411–16
128. Zeman P. 1988. Surface skin lipids of birds: a proper host kairomone and feeding inducer in the poultry red mite, *Dermanyssus gallinae*. *Exp. Appl. Acarol.* 5:163–73
129. Zindel R, Gottlieb Y, Aebi A. 2011. Arthropod symbioses: a neglected parameter in pest- and disease-control programmes. *J. Appl. Ecol.* 48:864–72
130. Schicht S, Qi W, Poveda L, Strube C. 2013. The predicted secretome and transmembranome of the poultry red mite *Dermanyssus gallinae*. *Parasites Vectors* 6:259
131. Schicht S, Qi W, Poveda L, Strube C. 2013. Whole transcriptome analysis of the poultry red mite *Dermanyssus gallinae* (De Geer, 1778). *Parasitology* 18:1–11



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